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# A guide to the Thalassinidea (Crustacea: Malacostraca: Decapoda) of the South Atlantic Bight

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NOAA Professional Paper NMFS 8

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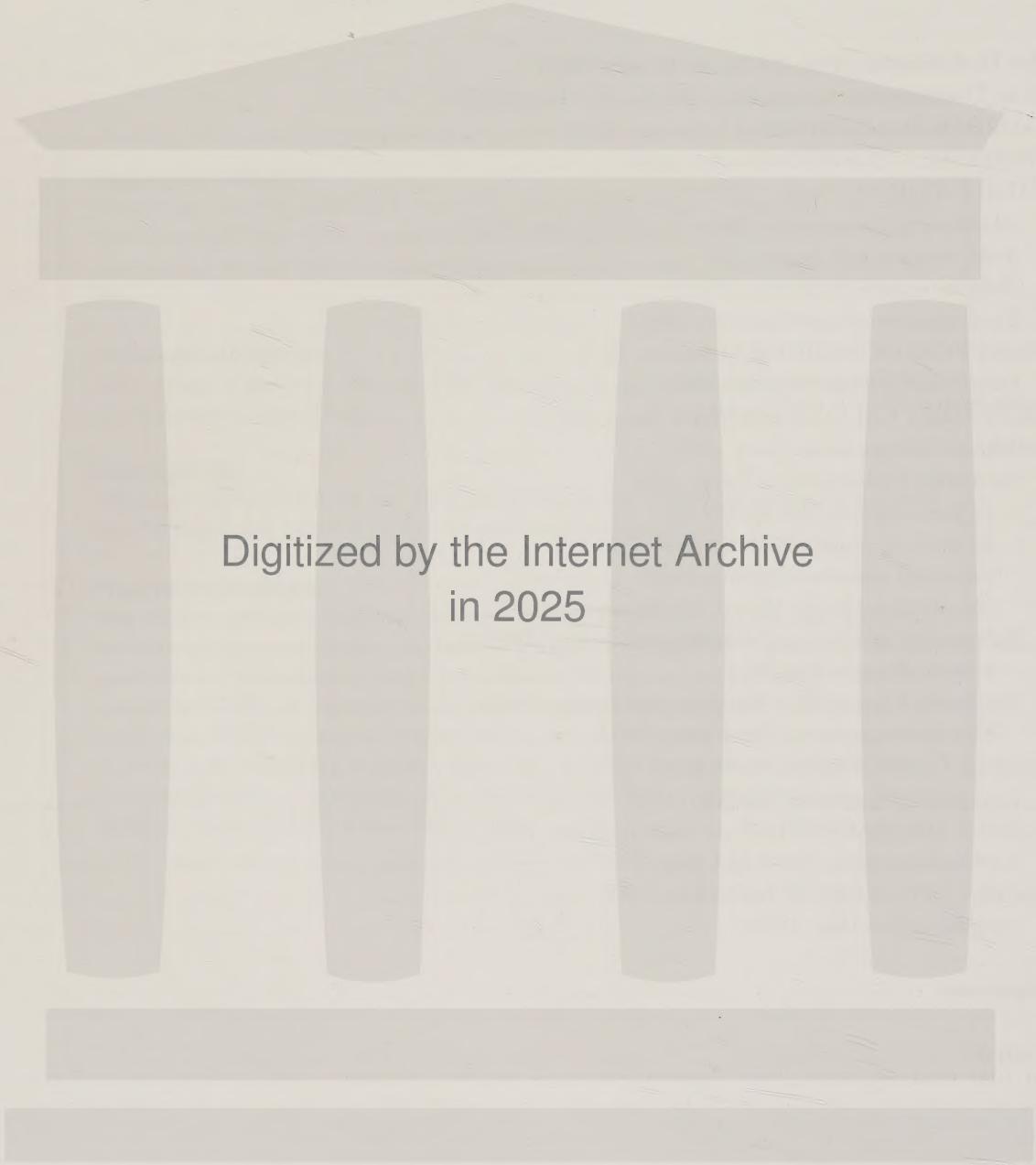

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**Abstract.** Ghost shrimp and mud shrimp in the decapod infraorder Thalassinidea are ecologically important members of many benthic intertidal and shallow subtidal infaunal communities, largely due to the sediment filtration and mixing that result from their burrowing and feeding behavior. These activities considerably modify their immediate environment and have made these cryptic animals extremely interesting to scientists in terms of their behavior, ecology, and classification.

Over 20 years ago, seven species of thalassinideans were known from the South Atlantic Bight (Cape Hatteras, NC to Cape Canaveral, FL). During this study, the examination of extensive collections from the National Museum of Natural History (NMNH), the Southeastern Regional Taxonomic Center (SERTC), and regional institutions, resulted in the identification of 14 species of thalassinideans currently known to occur within this region. The family Axiidae is represented by three species: *Axius armatus, Calaxius jenneri,* and *Paraxiopsis gracilimana*; the Callianassidae by six: *Biffarius biformis, B. cf. fragilis, Callichirus major, Cheramus marginatus, Gilvossius setimanus,* and *Necallianassa berylae*; the Calocarididae by two: *Calocaris templemani* and *Acanthaxius hirsutimanus*; and the families Laomediidae, Thomassiniidae, and Upogebiidae are each represented by one: *Naushonia crangonoides, Crosniera wennerae,* and *Upogebia affinis,* respectively. An illustrated key is presented for species level identification and supplemental notes on the ecology, distribution, and taxonomy of the species are provided.

# A guide to the Thalassinidea (Crustacea: Malacostraca: Decapoda) of the South Atlantic Bight

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## Introduction

Despite the fact that they are commonly referred to as ghost shrimp or mud shrimp, thalassinideans belong to a decapod crustacean infraorder that is more closely related to anomurans and crabs than to true shrimp. These burrowing animals are an important benthic component of sandy or muddy intertidal and shallow subtidal habitats worldwide (Griffis and Suchanek, 1991; Atkinson and Taylor, 2004). Although casual observers walking along the shore may notice the holes of thalassinidean burrows on tidal mud flats or sand bars, it is unlikely that many of them understand the significance of the animals within.

The actively burrowing lifestyle of thalassinideans and their filter feeding strategies result in high rates of sediment turnover. Using abdominal appendages that are specially modified, thalassinideans draw water into burrows that may be relatively simple "Y"- or "U"-shaped vertical tunnels, or much more elaborate systems of branching tunnels and chambers (Griffis and Suchanek, 1991). The animals' biofiltering activity disperses nutrients and oxygen throughout the surface sediments and also provides food that sustains them in their underground homes. Their burrowing and water circulation exert a large influence on the sediment structure and geochemistry of environments where they are abundant (Ziebis et al., 1996; Dworschak, 2000a; Dworschak et al., 2006). For that reason, these decapod crustaceans are fascinating to scientists, who are just beginning to understand their complex behavior, specialized morphology, and the evolutionary history of the infraorder.

This guide comprises a broad taxonomic assessment and review of the thalassinidean fauna of the South Atlantic Bight (SAB), which is defined here as the coastal and

oceanic region of the southeastern United States between Cape Hatteras, North Carolina and Cape Canaveral, Florida. This guide is further restricted to depths ranging from the intertidal zone to 200 m. Since the last broad taxonomic treatment of SAB thalassinideans (Williams, 1984) is now over 20 years old and missing many of the species currently known to occur within the SAB, it was clear that a taxonomic revision of SAB thalassinideans was needed.

The purpose of this study is to critically review previous information and studies, establish new regional records, document distributional records for the SAB, summarize the taxonomic information available on each species treated, and present an illustrated key for the identification of the Thalassinidea currently known from the inshore, nearshore, and offshore shelf waters of the SAB.

## Overview of the Thalassinidea

Currently, the Thalassinidea contains three superfamilies (Axioidea Huxley, 1879; Callianassoidea Dana, 1852; Thalassinoidea Latreille, 1831), whose members are widely distributed in estuarine and marine habitats throughout much of the world from the intertidal to depths exceeding 2500 m (Lemaitre and Ramos, 1992; Poore, 1997; Dworschak, 2000a; Dworschak, 2005).

Members of the infraorder Thalassinidea are highly specialized decapod crustaceans that construct and live in permanent burrows in sediment. These burrows can be highly complex, with multiple chambers, and the burrows of some species can exceed a depth of 2 m (Weimer and Hoyt, 1964; Griffis and Suchanek, 1991; Nickell and Atkinson, 1995; Tamaki and Ueno, 1998; Dworschak, 2000b; Kinoshita et al., 2003). Thalassinideans possess an elongate and flexible sub-cylindrical body (partly sclerotized in callianassids and upogebiids, more so in axiids); chelipeds, legs, and mouthparts adapted for locomotion, burrowing, and feeding; broad setose pleopods for pumping water through burrows; and broad uropods for sealing burrows (Bishop and Williams, 2005). Figure 1 shows the general morphology of a thalassinidean.

Several different feeding strategies have been recorded within the Thalassinidea: suspension feeding, deposit feeding, and scavenging (Griffis and Suchanek, 1991; Nickell and Atkinson, 1995; Abed-Navandi and Dworschak, 2005). Predation or carnivorous feeding behavior by the callianassid *Corallianassa longiventris* (A. Milne-Edwards, 1870) on other crustaceans has been observed during field studies in the Turks and Caicos (Heard, pers. observ.) Under laboratory conditions, however, this species appeared to exhibit deposit and herbivorous feeding behavior (Dworschak, 2005). The feeding and burrowing activity of thalassinideans has a great impact on the environment surrounding the burrows, given the high densities of many species and the large amounts of sediment re-working they cause. *Callianassa* species can filter as much as 2.59kg/$m^2$ of sediment per day (Suchanek, 1983), and *Biffarius biformis* Biffar, 1971a has been recorded at densities of 483 individuals/$m^2$ in St. Catherines Sound, Georgia (Bishop and Bishop, 1992).

Detailed treatments of the classification of Thalassinidea have been presented by Manning and Felder (1991a), Poore (1994), Tudge et al. (2000), Martin and Davis (2001), and Sakai (2005). While it is the most recent, Sakai's (2005) classification of the Infraorder Thalassinidea Latreille, 1831, has not yet been critically evaluated, and so we follow the classification presented by Martin and Davis (2001), which largely followed Poore (1994).

Members of the thalassinidean superfamilies Axioidea and Callianassoidea are found in the SAB. The Axioidea is composed of four families, two of which are represented in the SAB: the Axiidae Huxley, 1879 and the Calocarididae Ortmann, 1891. The Callianassoidea contains six families, four of which are represented in the SAB: Callianassidae Dana, 1852, Laomediidae Borradaile, 1903, Thomassinidae de Saint Laurent, 1979, and Upogebiidae Borradaile, 1903. The Thalassinoidea, a small group containing a single genus with a few species, is largely restricted to the western Pacific (Poore and Griffin, 1979; Dworschak, 1992) and is not known from the SAB.

## Previous records of thalassinideans from the South Atlantic Bight

The last comprehensive review of regional thalassinideans was in A. B. Williams' (1984) guide to shrimp, lobsters, and crabs of the Atlantic coast of the eastern United States. Williams (1984) recorded seven species from the South Atlantic Bight (*Callianassa major* Say, 1818; *Callianassa atlantica* Rathbun, 1926; *Callianassa biformis* Biffar, 1971a; *Axiopsis jenneri* (Williams, 1974); *Calocaris templemani* Squires, 1965; *Naushonia crangonoides* Kingsley, 1897; *Upogebia affinis* (Say, 1818)). Nizinski (2003) expanded the list to eight species with the addition of *Gilvossius setimanus* (De Kay, 1844) (=*Callianassa atlantica*) and *Necallianassa berylae* Heard and Manning, 1998, based on an extensive review of taxonomic literature published since 1984.

## Updated distributional records of thalassinideans from the South Atlantic Bight

Since Williams' (1984) comprehensive monograph on the Decapoda of the U.S. Atlantic coast, three new species have been described within the SAB (*Paraxiopsis*

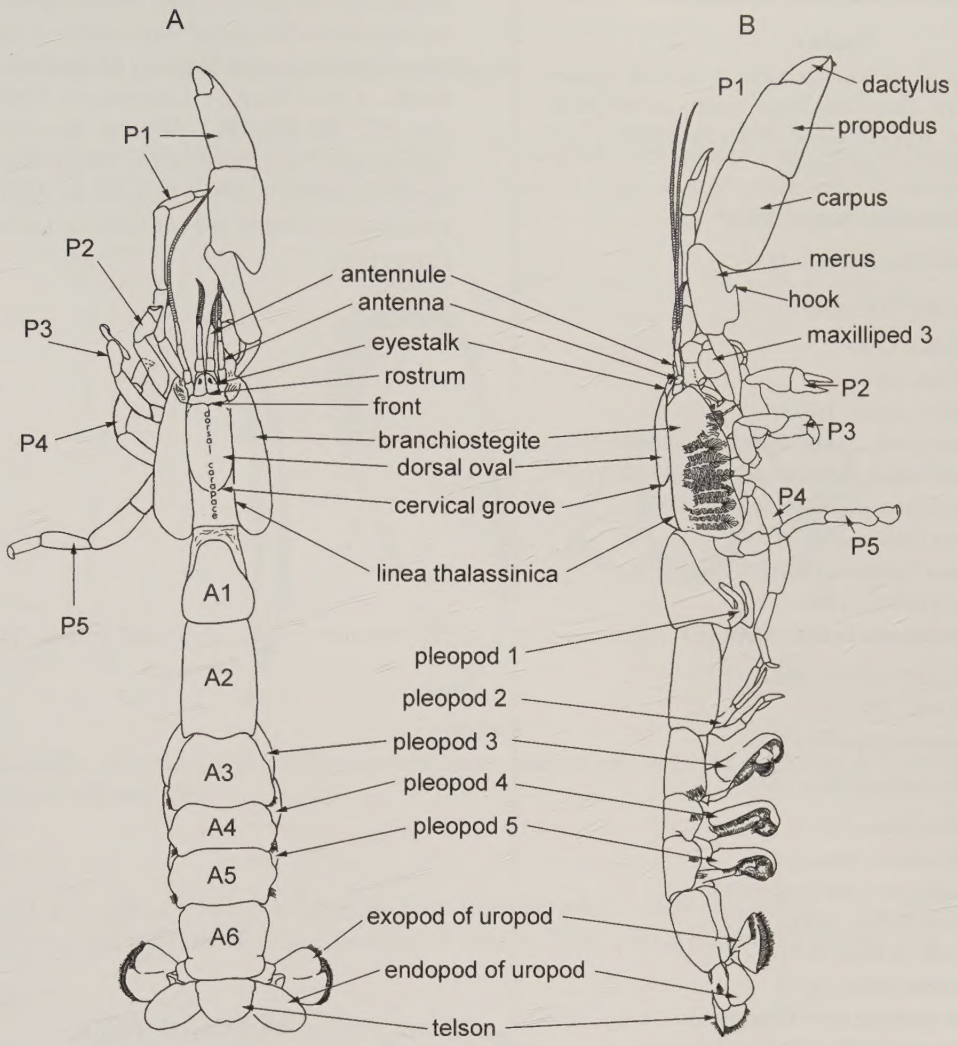


**Figure 1**

The general morphology of thalassinideans: (A) dorsal view; (B) lateral view. Modified from Biffar, 1971b. P1-5: pereopods 1–5; A1-6: abdominal segments 1–6.

*gracilimana* Kensley, 1996, *Necallianassa berylae* Heard and Manning, 1998, and *Crosniera wennerae* Heard and King, 2007), and a range extension of *Axius armatus* S. I. Smith, 1881 was reported (Kensley, 2001). Range extensions of four more species, *Acanthaxius hirsutimanus* (Boesch and Smalley, 1972), *Calaxius jenneri* (Williams, 1974), *Cheramus marginatus* (Rathbun, 1901), and *Necallianassa berylae* are recorded here. Thus, we report here that 14 species of thalassinideans occur within the SAB. Table 1 gives a systematic listing of the Thalassinidea known from the SAB.

There have been a number of taxonomic changes within the Thalassinidea since Williams (1984) that have been adopted here. A taxonomic listing of the species within the Thalassinidea currently known from the SAB is given in Table 1.

## Materials and methods

We examined scientific publications, "gray literature" (e.g. regional agency technical reports, contract reports, etc.), and collections from the region (National Museum of Natural History, Smithsonian Institution, Washington, DC; Duke Marine Laboratory, Beaufort, NC; Grice Marine Laboratory, Charleston, SC; South Carolina Department of Natural Resources, Charleston, SC; and University of Louisiana at Lafayette, LA), to produce a comprehensive list of thalassinidean species from the SAB. Wherever possible, we verified these records by re-examining the specimens reported.

The following abbreviations have been used: **USNM**—United States National Museum, now known as the National Museum of Natural History (NMNH),

**Table 1**

A systematic listing of Thalassinidea currently known from the inshore, shelf, and slope waters of the SAB. (*), new taxon reports since Williams (1984); (+), range extensions; (=), synonyms.

**Order** Decapoda Latrielle, 1802

**Infraorder** Thalassinidea Latreille, 1831

**Superfamily** Axioidea Huxley, 1879

**Family** Axiidae Huxley, 1879
- Genus *Axius* Leach, 1815
  - ***Axius armatus*** S. I. Smith, 1881*+
- Genus *Acanthaxius* Sakai and de Saint Laurent, 1989
  - ***Acanthaxius hirsutimanus*** (Boesch and Smalley, 1972)* +
- Genus *Calaxius* Sakai and de Saint Laurent, 1989
  - ***Calaxius jenneri*** (Williams, 1974)* +
  - =*Axiopsis jenneri* (Williams, 1974)
- Genus *Paraxiopsis* DeMan, 1905
  - ***Paraxiopsis gracilimana*** Kensley, 1996*

**Family** Calocarididae Ortmann, 1891
- Genus *Calocaris* Bell, 1853
  - ***Calocaris templemani*** Squires, 1965

**Superfamily** Callianassoidea Dana, 1852

**Family** Callianassidae Dana, 1852
- Subfamily Callianassinae Dana, 1852
- Genus *Biffarius* Manning and Felder 1991a
  - ***Biffarius biformis*** (Biffar, 1971a)
  - =*Callianassa biformis* Biffar, 1971a
  - ***Biffarius cf. fragilis*** (Biffar, 1970)
- Genus *Gilvossius* Manning and Felder, 1991b
  - ***Gilvossius setimanus*** (DeKay, 1844)
  - =*Callianassa atlantica* Rathbun, 1926
- Genus *Necallianassa* Heard and Manning, 1998
  - ***Necallianassa berylae*** Heard and Manning, 1998*+
- Subfamily Callichirinae Manning and Felder, 1991a*
- Genus *Callichirus* Stimpson, 1866
  - ***Callichirus major*** (Say, 1818)
- Subfamily Cheraminae Manning and Felder, 1991a*
- Genus *Cheramus* Bate, 1888
  - ***Cheramus marginatus*** (Rathbun, 1901)* +
  - =*Callianassa marginata* Rathbun, 1901

**Family** Laomediidae Borradaile, 1903
- Genus *Naushonia* Kingsley, 1897
  - ***Naushonia crangonoides*** Kingsley, 1897

**Family** Thomassiniidae de Saint Laurent, 1979
- Genus *Crosniera* Kensley and Heard, 1991
  - ***Crosniera wennerae*** Heard and King, 2007*

**Family** Upogebiidae Borradaile, 1903
- Genus *Upogebia* Leach, 1814
  - ***Upogebia affinis*** (Say, 1818)

Smithsonian Institution, Washington DC; **SERTC**—Southeastern Regional Taxonomic Center, South Carolina Department of Natural Resources, Charleston, SC; **GML**—Grice Marine Laboratory, College of Charleston, SC; **MARMAP**— Marine Resources Monitoring Assessment and Prediction Program, South Carolina Department of Natural Resources, Charleston, SC; and **ULLZ**—University of Louisiana at Lafayette, Zoological Collection.

## Results

### Key to the Thalassinidea from the South Atlantic Bight

1. Pereopod 1 strongly subchelate (dactylus articulated to fold back against the ventral margin of the propodus). Uropodal endopod and exopod each with distinct distal suture. Pereopod 2 simple (not chelate) (Fig. 2). . . . . ***Naushonia crangonoides*** Kingsley, 1897

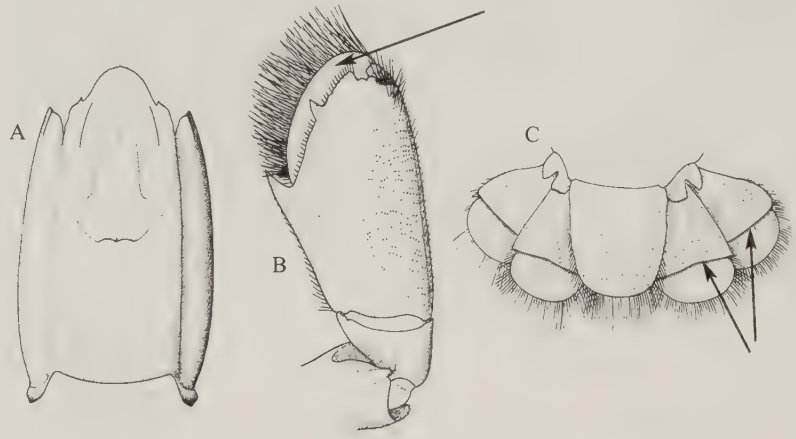


**Figure 2**

*Naushonia crangonoides*: (A) dorsal view of carapace; (B) inner surface of pereopod 1 (chela); (C) telson and uropods. A–C: modified from Williams, 1984.

—Pereopod 1 strongly or weakly chelate (dactylus forming pincer with propodus). Uropodal endopod lacking distal suture; exopod with distal suture present or absent. Pereopod 2 chelate or simple (Fig. 3). . . . . **2**

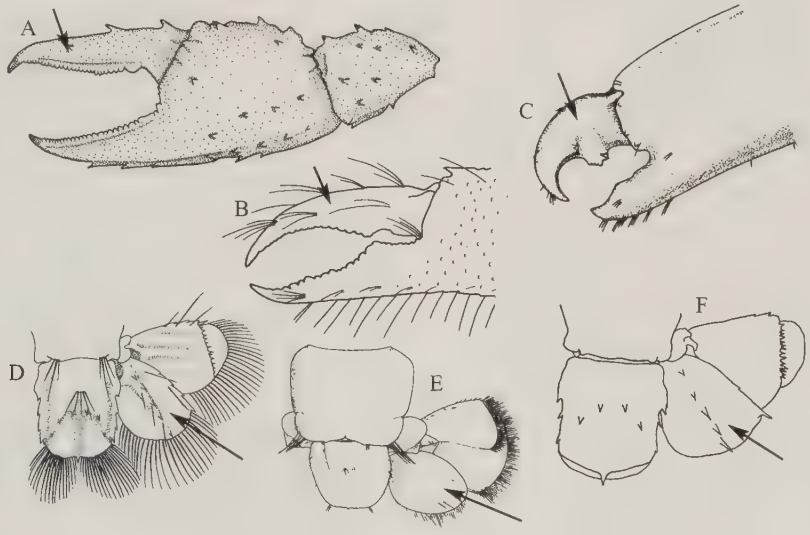


**Figure 3**

(A) *Acanthaxius hirsutimanus*: pereopod 1 (chela); (B) *Paraxiopsis gracilimana*: distal end of pereopod 1 (chela); (C) *Callichirus major*: distal end of pereopod 1 (chela); (D) *Paraxiopsis gracilimana*: telson and uropods; (E) *Gilvossius setimanus*: telson and uropods; (F) *Acanthaxius hirsutimanus*: telson and uropods. A, F: modified from Boesch and Smalley, 1972; C, E: Modified from Williams, 1984; B, D: modified from Kensley, 1996.

2. Rostrum well developed, spinose, either rounded or acutely tipped. Eyestalks rounded. Pereopod 3 not highly modified: similar to pereopods 4 and 5. Pleopods 2–5 setose, well developed (Fig. 4). . . . . 3

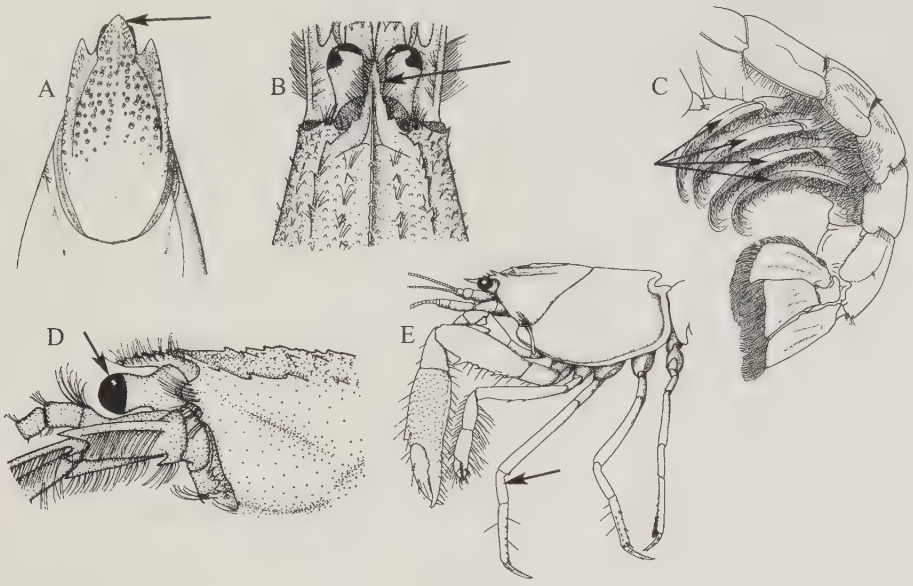


**Figure 4**

(A) *Upogebia affinis*: dorsal view of carapace showing rostrum; (B) *Acanthaxius hirsutimanus*: dorsal view of anterior carapace showing rostrum; (C) *Upogebia affinis*: lateral view of abdomen showing pleopods; (D) *Acanthaxius hirsutimanus*: lateral view of anterior carapace showing eyestalks; (E) *Paraxiopsis gracilimana*: lateral view of cephalothorax showing pereopods 1–5. A: modified from Williams, 1984; B, D: modified from Boesch and Smalley, 1972; C: modified from Williams, 1993; E: modified from Kensley, 1996.

—Rostrum small, usually triangular, flattened, dorsally smooth. Eyestalks flattened dorsoventrally. Pereopod 3 highly modified, propodus usually broadly expanded and distinctly different from pereopods 4 and 5. Pleopods 1–2 reduced; pleopods 3–5 well developed with broad, highly setose rami (Fig. 5). . . . . 8

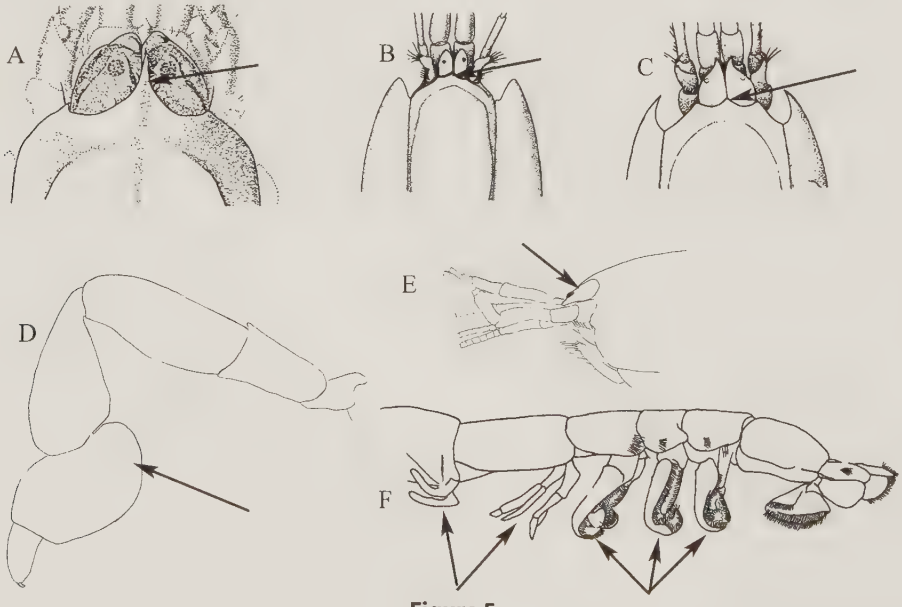


**Figure 5**

(A) *Necallianassa berylae*: dorsal view of anterior carapace showing rostrum; (B) *Callichirus major*: dorsal view of anterior carapace showing rostrum; (C) *Gilvossius setimanus*: dorsal view of anterior carapace showing rostrum; (D) *Biffarius biformis*: pereopod 3; (E) *Biffarius biformis*: lateral view of anterior carapace showing flattened eyestalks; (F) lateral view of generalized thalassinidean showing pleopods 1 and 2 reduced. A: modified from Heard and Manning, 1998; B, C: modified from Williams, 1984; D, E: original illustrations by R.W. Heard; F: modified from Biffar, 1971b.

3. Pereopod 1 strongly subchelate, superficially appearing chelate, but having short fixed finger (distal extension of propodus). Pereopod 2 simple (not chelate), similar to pereopods 3–4. Rostrum large, spinose, broadly rounded to a blunt tip (Fig. 6). . . . . ***Upogebia affinis*** (Say, 1818)

**Figure 6**

*Upogebia affinis*: (A) lateral view of whole animal; (B) detail of dactyl of pereopod 2; (C) dorsal view of carapace; (D) pereopod 1 (chela) showing weakly chelate form. A, B: modified from Williams, 1993; C, D: modified from Williams, 1984.

—Pereopod 1 strongly chelate. Pereopod 2 chelate. Rostrum triangular, laterally spinose, acutely tipped (Fig. 7). . . . . 4

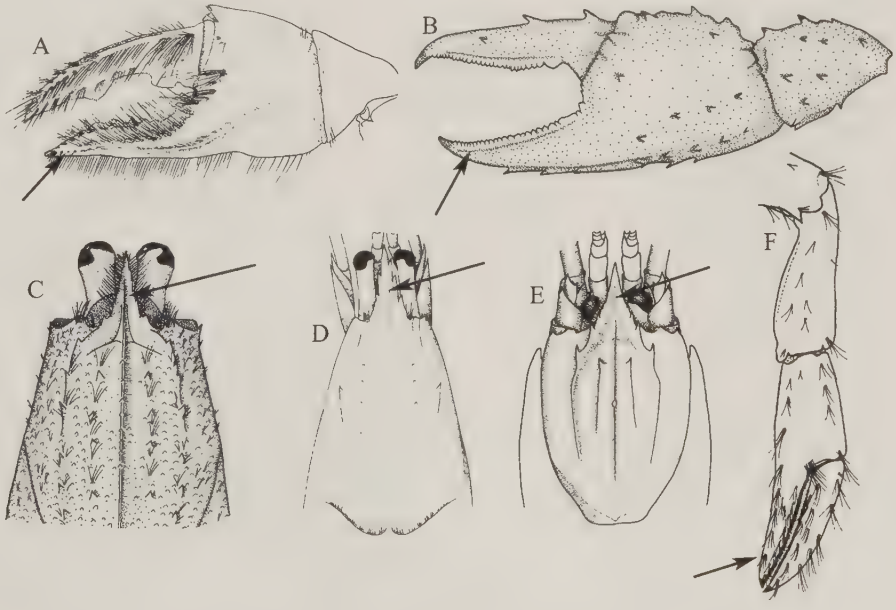


**Figure 7**

(A) *Calocaris templemani*: pereopod 1 (chela); (B) *Acanthaxius hirsutimanus*: pereopod 1 (chela); (C) *Acanthaxius hirsutimanus*: dorsal view of anterior carapace showing rostrum; (D) *Calaxius jenneri*: dorsal view of anterior carapace showing rostrum; (E) *Paraxiopsis gracilimana*: dorsal view of anterior carapace showing rostrum; (F) *Acanthaxius hirsutimanus*: pereopod 2. A, D: modified from Williams, 1984; B, C, F: modified from Boesch and Smalley, 1972; E: modified from Kensley, 1996.

4. Eyes with pigment indistinct (diffuse or appearing absent); eyestalk rudimentary, flattened obliquely on distal surface. Uropodal exopod with weakly defined distal suture, recognizable part of suture margin lacking spines; endopod with medial carina unarmed (lacking spines). Family Calocariidae (Fig. 8). . . . . ***Calocaris templemani*** Squires, 1965

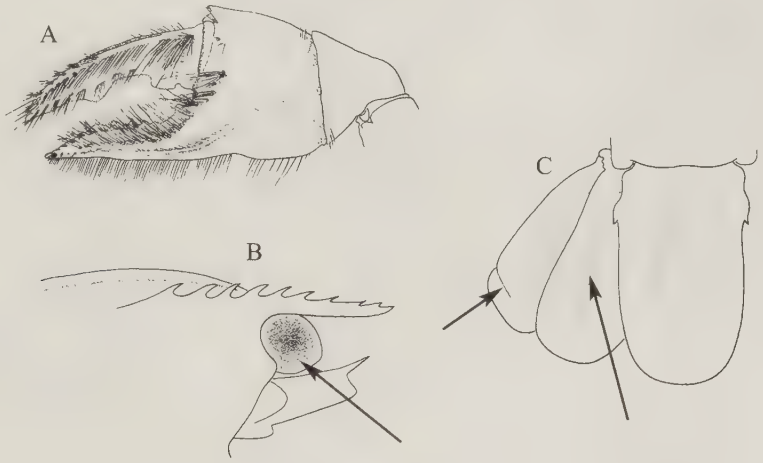


**Figure 8**

*Calocaris templemani*: (A) pereopod 1 (chela); (B) lateral view of anterior carapace; (C) telson and uropods. A–C: modified from Williams, 1984.

—Eyes with eyestalk well developed, nearly reaching and sometimes overreaching tip of rostrum. Uropodal exopod with well-defined distal suture, suture margin armed with spines; endopod with medial carina armed with several distinct spines. Family Axiidae (Fig. 9). . . . . **5**

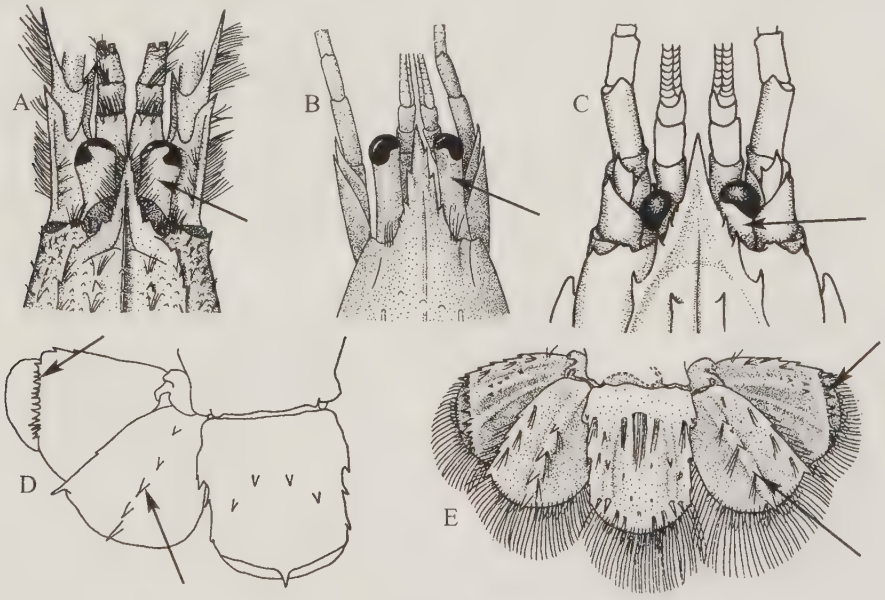


**Figure 9**

(A) *Acanthaxius hirsutimanus*: dorsal view of anterior carapace; (B) *Calaxius jenneri*: dorsal view of anterior carapace; (C) *Paraxiopsis gracilimana*: dorsal view of anterior carapace; (D) *Acanthaxius hirsutimanus*: telson and uropods; (E) *Calaxius jenneri*: telson and uropods. A, D: modified from Boesch and Smalley, 1972; B, E: modified from Williams, 1984; C: modified from Kensley, 1996.

5. Pereopod 1 major or minor chela with dactylus distinctly longer than the palm (proximal part of propodus), dorsal margin of dactylus with a few sharp spines. Eyes extending slightly beyond rostrum. Carapace dorsal surface distinctly setose, granulose, and spinose; lateral carina with 5 or more spines (Fig. 10). . . . . ***Acanthaxius hirsutimanus*** (Boesch and Smalley, 1972)

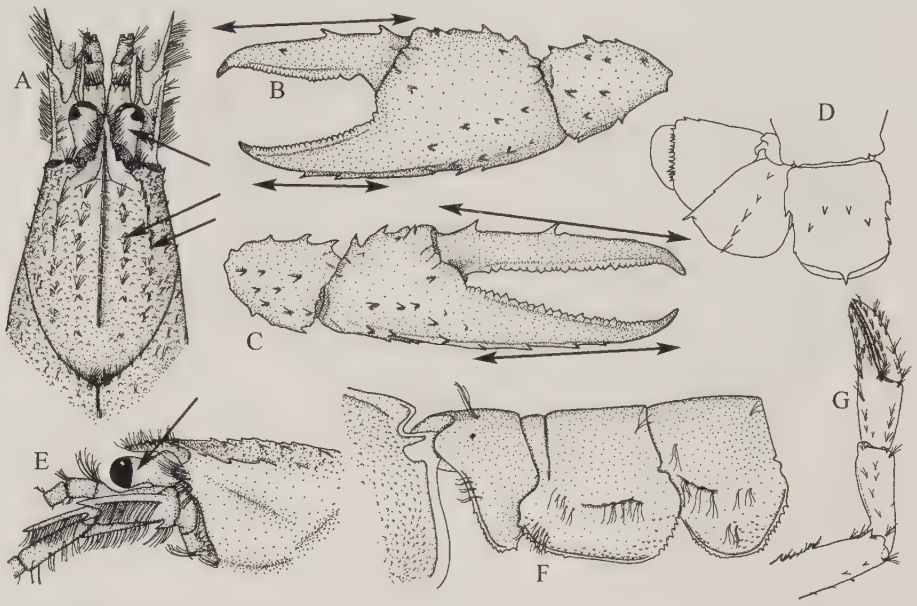


**Figure 10**

*Acanthaxius hirsutimanus*: (A) dorsal view of anterior carapace; (B) pereopod 1 major (left) chela; (C) pereopod 1 minor (right) chela; (D) telson and uropods; (E) lateral view of anterior carapace; (F) lateral view of posterior part of carapace and first three abdominal segments; (G) pereopod 2. A–G: modified from Boesch and Smalley, 1972.

—Pereopod 1 major and minor chelae with dactylus a similar length to or shorter than the palm (proximal part of the propodus), dorsal margin of dactylus smooth, or nearly so. Eyes not extending beyond rostrum. Carapace dorsal surface weakly to moderately setose; lateral carina with 4 or fewer spines (Fig. 11). . . . . **6**

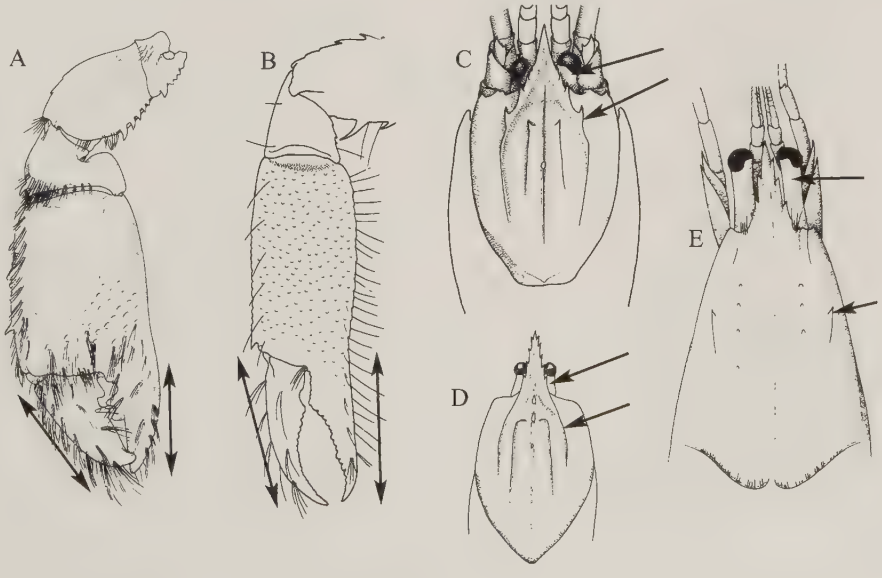


**Figure 11**

(A) *Calaxius jenneri*: pereopod 1 (chela); (B) *Paraxiopsis gracilimana*: pereopod 1 (chela); (C) *Paraxiopsis gracilimana*: dorsal view of anterior carapace; (D) *Axius armatus*: dorsal view of anterior carapace; (E) *Calaxius jenneri*: dorsal view of anterior carapace. A, E: modified from Williams, 1984; B, C: modified from Kensley, 1996; D: modified from Kensley, 2001.

6. Carapace dorsal surface with indistinct lateral and submedial carinae; lateral carinae indicated by a single strong spine (not noticeably coalescing to form rostral margin). Pereopod 1 major chela masive, densely setose. Telson without medial spine on distal margin (Fig. 12)..... ***Calaxius jenneri*** (Williams, 1974)

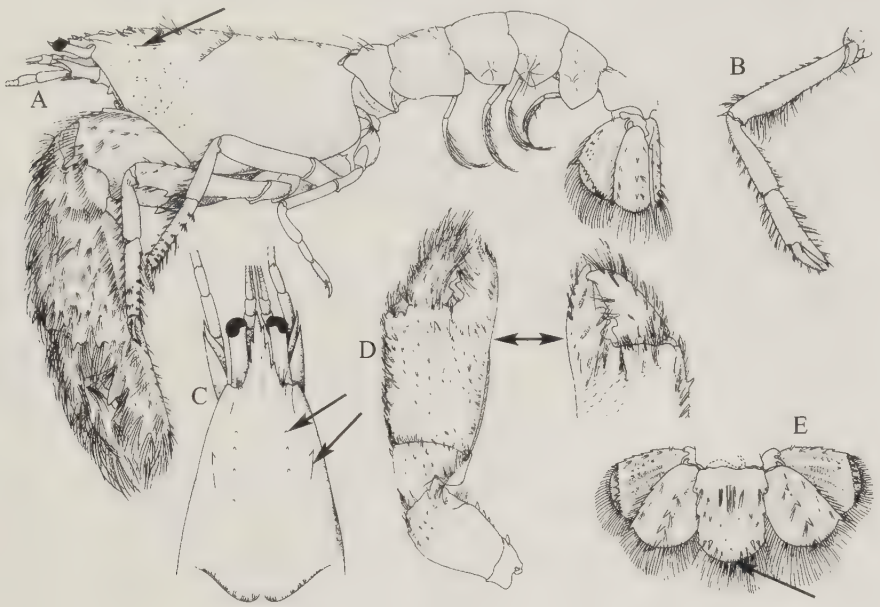


**Figure 12**

*Calaxius jenneri*: (A) lateral view of whole animal; (B) pereopod 2; (C) dorsal view of anterior carapace; (D) pereopod 1 major (right) chela; (E) telson and uropods. A–E: modified from Williams, 1984.

—Carapace dorsal surface with distinct lateral, submedial, and medial carinae; lateral carinae extending anteriorly to coalesce and form rostral margin. Pereopod 1 major chela not massive or exceptionally setose. Telson with medial spine present on distal margin (Fig. 13)..... **7**

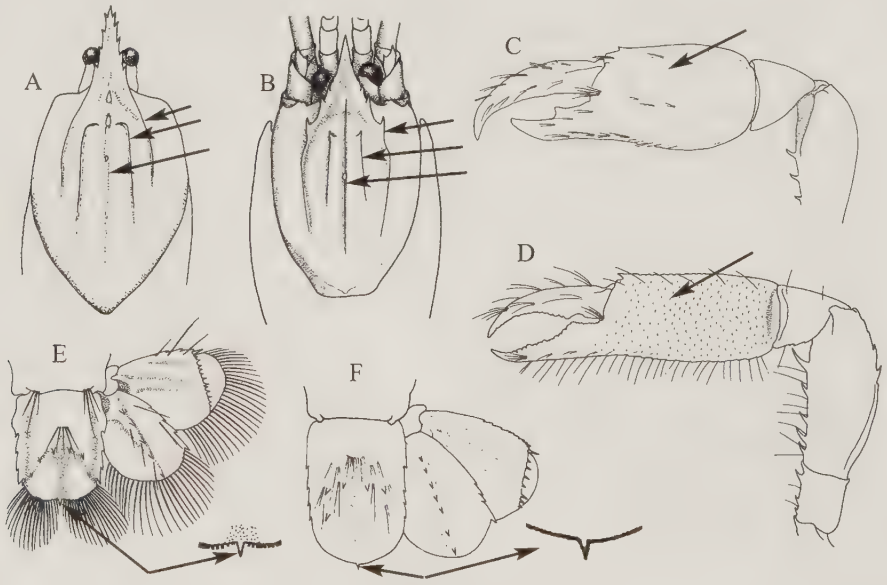


**Figure 13**

(A) *Axius armatus*: dorsal view of anterior carapace; (B) *Paraxiopsis gracilimana*: dorsal view of anterior carapace; (C) *Axius armatus*: pereopod 1 major chela; (D) *Paraxiopsis gracilimana*: pereopod 1 major chela; (E) *Paraxiopsis gracilimana*: telson and uropods; (F) *Axius armatus*: telson and uropods. A, C, F: modified from Kensley, 2001; B, D, E: modified from Kensley, 1996.

7. Carapace medial carina lacking spines; submedial carinae each with distinct spine anteriorly; each lateral carina with an anterior spine (situated posterior to, and merging with, the rostrum); rostrum with 4–6 progressively smaller lateral spines and associated setae, anterior half smooth or with inditinct spines and small setae (Fig. 14). . . . . ***Paraxiopsis gracilimana*** Kensley, 1996

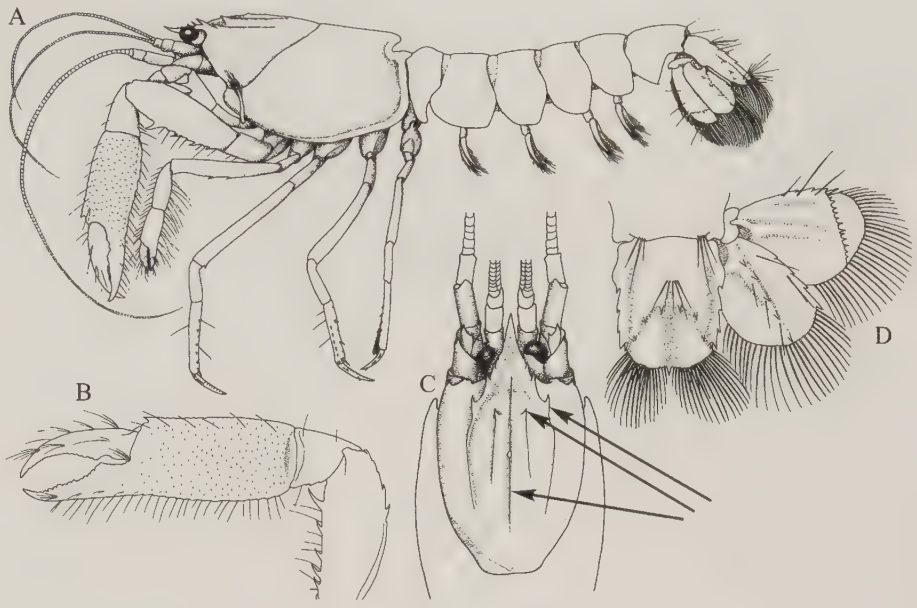


**Figure 14**

*Paraxiopsis gracilimana*: (A) lateral view of whole animal; (B) pereopod 1 (chela); (C) dorsal view of anterior carapace; (D) telson and uropods. A–D: modified from Kensley, 1996.

—Carapace medial carina armed anteriorly with 1–3 spines; submedial carinae lacking spines; lateral carinae lacking spines; rostrum with 3–6 pairs of distinct similarly sized lateral spines, continuing to tip (Fig. 15). . . . . ***Axius armatus*** S. I. Smith, 1881

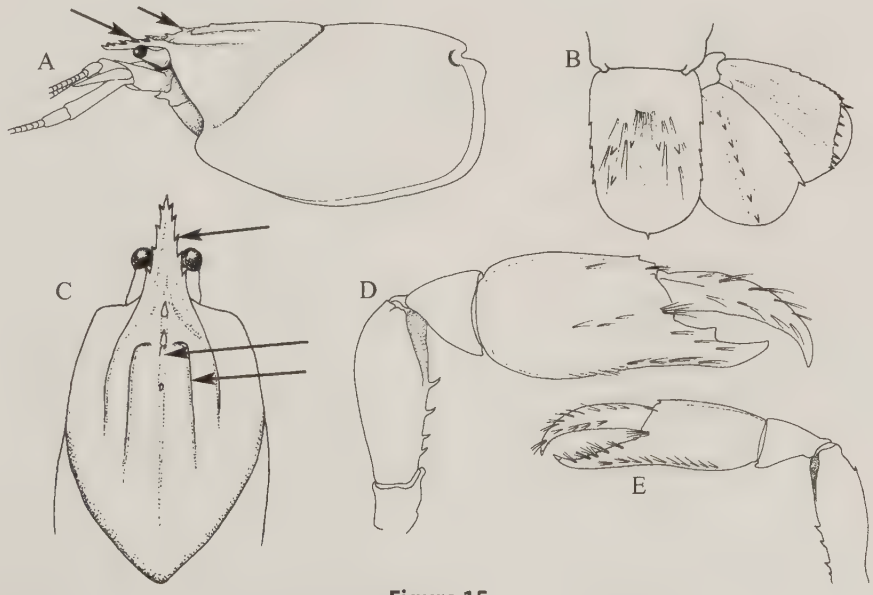


**Figure 15**

*Axius armatus*: (A) lateral view of carapace; (B) telson and uropods; (C) dorsal view of anterior carapace; (D) pereopod 1 major chela; (E) pereopod 1 minor chela. A–E: modified from Kensley, 2001.

8. Pereopod 3 propodus distal margin with single spiniform seta. Maxilla 2 with long distinctive seta on posterior lobe of scaphognathite. Uropodal exopod with broadly rounded margin, not appearing bilobed. Family Thomassiniidae (Fig. 16). ..... ***Crosniera wennerae*** Heard and King, 2007

**Figure 16**

*Crosniera wennerae*: (A) lateral view of carapace; (B) uropods and telson; (C) pereopod 3 showing spiniform seta including enlargement with fine setae removed; (D) maxilla 2 with long seta. A–D: original illustrations by R.W. Heard.

—Pereopod 3 propodus distal margin lacking spiniform seta. Maxilla 2 lacking long distinctive seta on posterior lobe of scaphognathite. Uropodal exopod appearing bilobed, with subdistal fringe of setae. Family Callianassidae (Fig. 17). ..... **9**

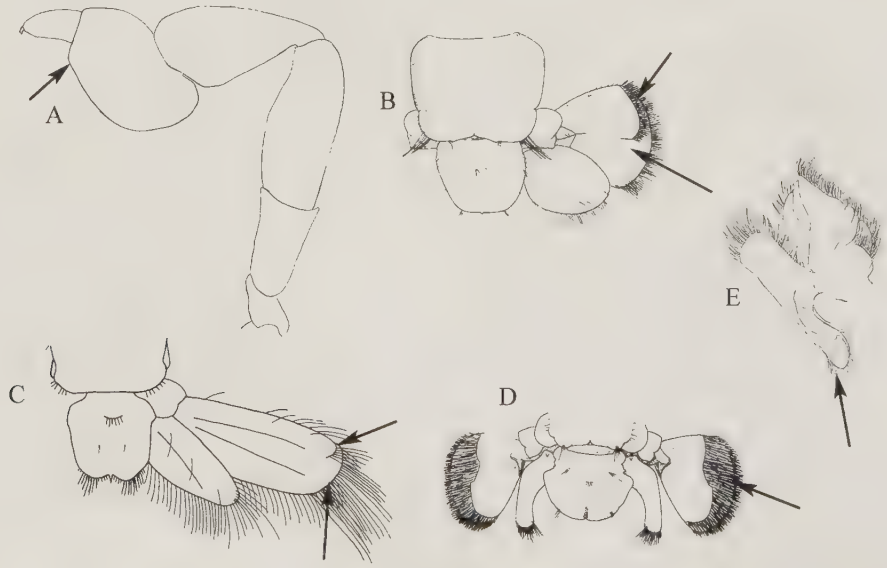


**Figure 17**

(A) *Biffarius biformis*: pereopod 3; (B) *Gilvossius setimanus*: telson and uropods; (C) *Cheramus marginatus*: telson and uropods; (D) *Callichirus major*: telson and uropods; (E) *Biffarius biformis*: maxilla 2 without seta. A, E: original illustrations by R.W. Heard; B, D: modified from Williams, 1984; C: modified from Biffar, 1971b.

**9.** Uropodal exopod at least twice as long as wide and nearly twice as long as telson; subdistal plates indistinct, appearing absent, represented by row of stout spiniform setae immediately behind distal fringe of plumose setae on distal upper margin. Pleopods 3–5 with finger-like appendices internae on endopod. Pereopod 1 (major chela) merus lower margin convex, smooth, lacking hook-like process or small spines. Subfamily Cheraminae (Fig. 18). . . . . ***Cheramus marginatus*** (Rathbun, 1901)

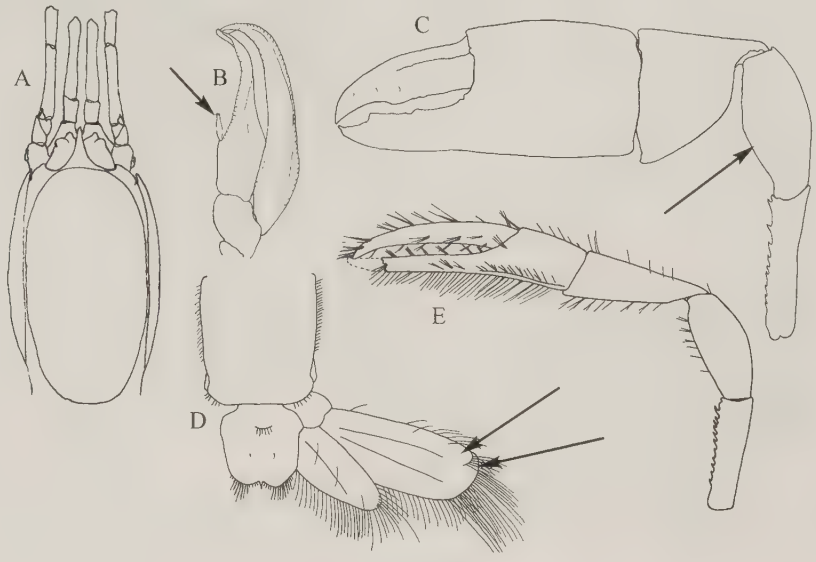


**Figure 18**

*Cheramus marginatus*: (A) dorsal view of carapace; (B) male pleopod 3 with appendix interna; (C) pereopod 1 major chela; (D) telson and uropods; (E) pereopod 1 minor chela. A–C: modified from Manning and Felder, 1991a; D–E: modified from Biffar, 1971b.

—Uropodal exopod distinctly less than twice as long as wide; subdistal plates distinct, with distal fringe of setae. Pleopods 3–5 having short stubby-like or embedded appendices internae on endopod. Pereopod 1 (major chela) merus lower margin with hook-like process or spine. Subfamilies Callianassinae and Callichirinae) (Fig. 19). . . **10**

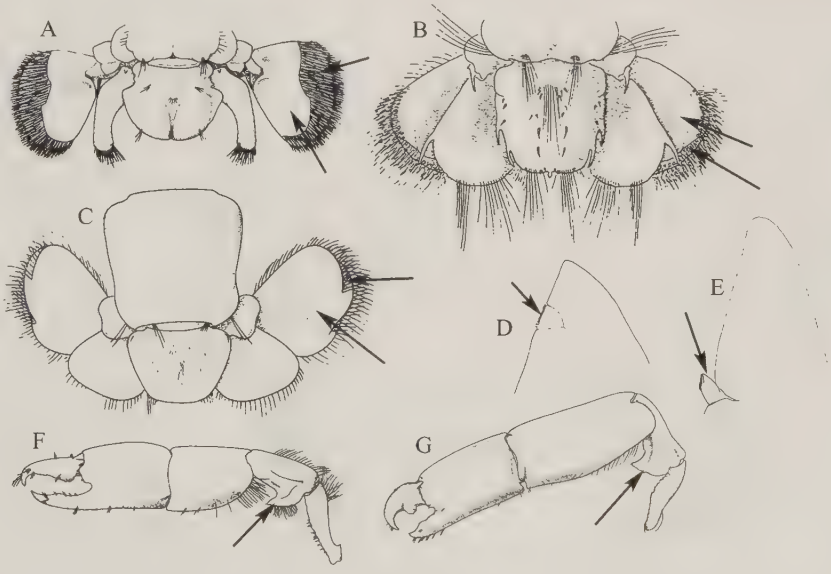


**Figure 19**

(A) *Callichirus major*: telson and uropods; (B) *Necallianassa berylae*: telson and uropods; (C) *Biffarius biformis*: telson and uropods; (D) tip of pleopod showing embedded appendix interna for *Callichirus* species; (E) tip of pleopod 3 showing stubby appendix interna for *Callianassa* species; (F) *Biffarius biformis*: pereopod 1 major chela; (G) *Callichirus major*: pereopod 1 major chela. A, C, F, G: modified from Williams, 1984; B: modified from Heard and Manning, 1998; D, E: modified from Manning and Felder, 1991a.

**10.** Uropodal endopod lateral margin with one large spine. Telson lateral margins with 2 spines (Fig. 20). ..... ***Necallianassa berylae*** Heard and Manning, 1998

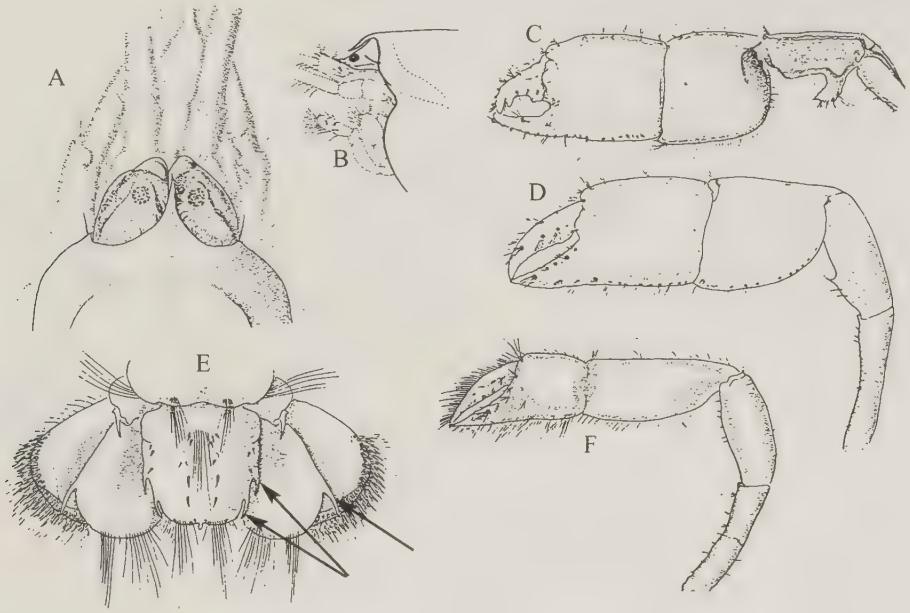


**Figure 20**

*Necallianassa berylae*: (A) dorsal view of anterior carapace; (B) lateral view of anterior carapace; (C) pereopod 1 major chela of male; (D) pereopod 1 minor chela of male (similar to major chela of female); (E) telson and uropods; (F) pereopod 1 minor chela of female. A–F: modified from Heard and Manning, 1998.

—Uropodal endopod lateral margin without spines. Telson lateral margins without spines (Fig. 21)..... **11**

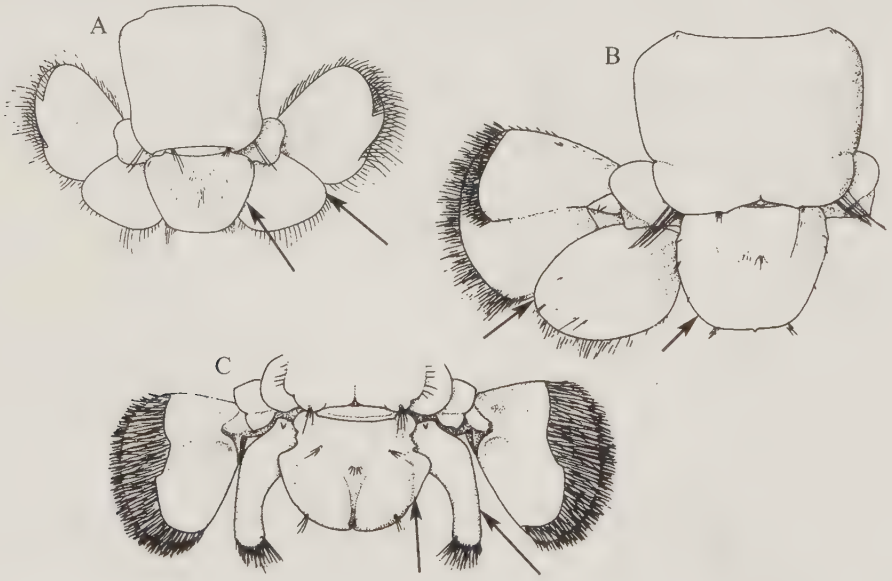


**Figure 21**

Telson and uropods: (A) *Biffarius biformis*; (B) *Gilvossius setimanus*; (C) *Callichirus major*. A–C: modified from Williams, 1984.

11. Uropodal endopod narrow, length four times width. Telson with distinct medial groove (Fig. 22). ..... ***Callichirus major*** (Say, 1818)

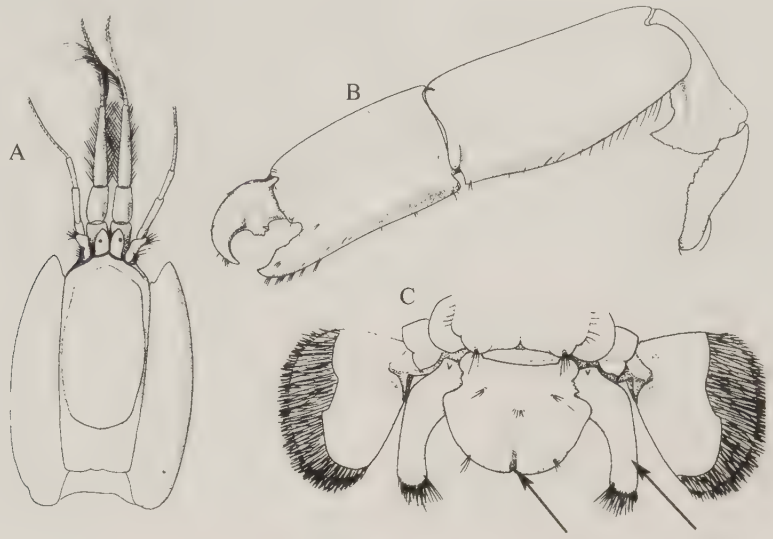


**Figure 22**

*Callichirus major*: (A) dorsal view of carapace: (B) pereopod 1 major (right) chela; (C) telson and uropods. A–C: modified from Williams, 1984.

—Uropodal endopod rounded, length less that two times width. Telson lacking distinct medial groove (Fig. 23) ..... 12

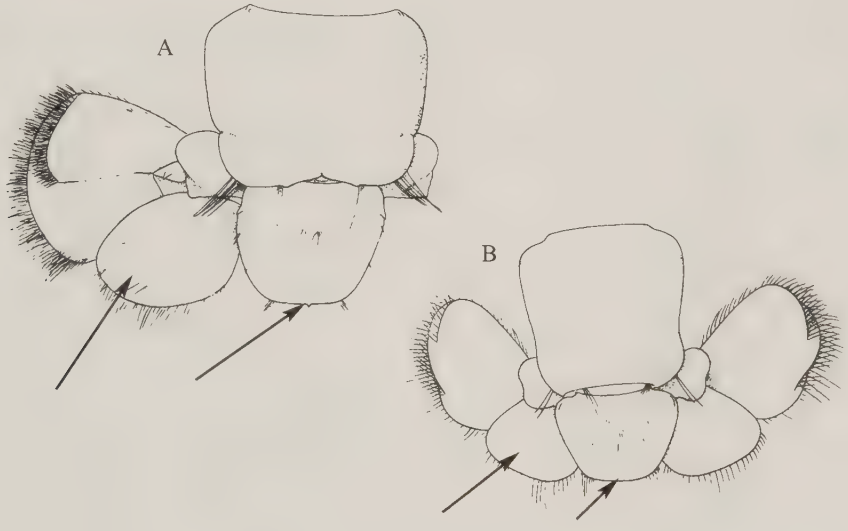


**Figure 23**

Telson and uropods: (A) *Gilvossius setimanus*; (B) *Biffarius biformis*. A, B: modified from Williams, 1984.

12. Eyestalks flattened and pointed, curving laterally at apex. Telson posterior margin with small acute spine medially (Fig. 24) ..... ***Gilvossius setimanus*** (DeKay, 1844)

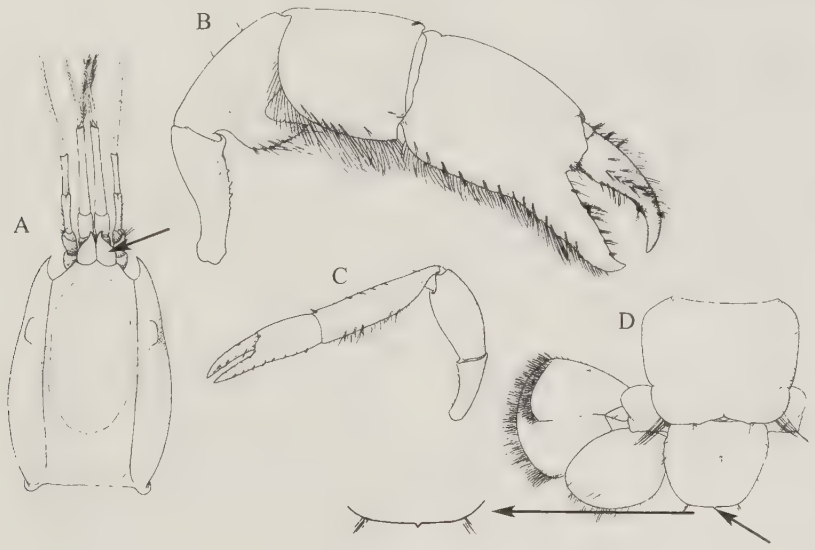


**Figure 24**

*Gilvossius setimanus*: (A) dorsal view of carapace; (B) pereopod 1 major (right) chela; (C) pereopod 1 minor (left) chela; (D) telson and uropods, with enlargement of spine on telson. A–D: modified from Williams, 1984.

—Eyestalks rounded at apex. Telson posterior margin lacking spine (Fig. 25) ..... 13

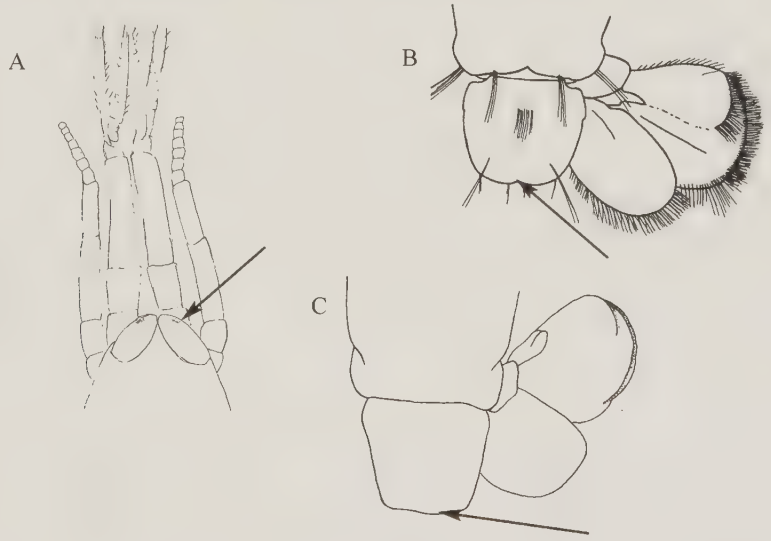


**Figure 25**

(A) *Biffarius cf. fragilis*: dorsal view of anterior carapace showing rounded eye stalks; (B) *Biffarius cf. fragilis*: telson and uropods; (C) *Biffarius biformis*: telson and uropods. A: original illustration by R. W. Heard; B: modified from Biffar, 1971b; C: modified from Manning and Felder, 1991a.

13. Antenna 1 peduncle distinctly shorter than antenna 2 peduncle. Pereopod 1 minor chela of male similar in size and shape to major and minor chelae of female, merus with weak hook-like spine; carpus about three times longer than wide at greatest width. Telson posterolateral corners with two, small, short spiniform setae; posterior margin fringed with row of closely spaced, plumose setae (Fig. 26) . . . . . ***Biffarius biformis*** (Biffar, 1971a)

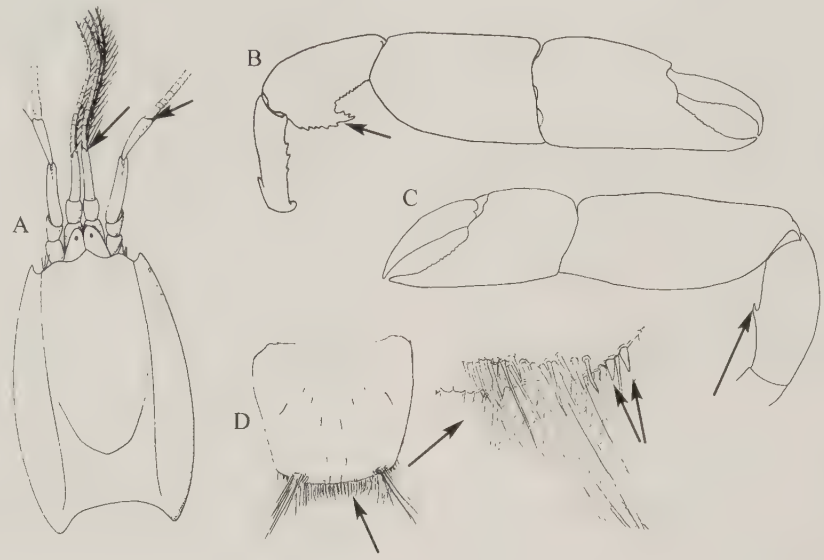


**Figure 26**

*Biffarius biformis*: (A) dorsal view of carapace; (B) pereopod 1 major chela; (C) pereopod 1 minor chela; (D) telson, with enlargement of posterolateral corner of telson. A: modifed from Williams, 1984; B, C: modified from Manning and Felder, 1991a; D: original illustration by R. W. Heard.

—Antenna 1 peduncle equal to, or slightly longer than, antenna 2 peduncle. Pereopod 1 major chela of female distinctly larger and more developed than minor chela; minor chela of male and female markedly elongate; merus lacking weak hook-like spine; carpus narrow, 5–6 times longer than greatest width. Telson posterolateral corners lacking setae or with a single, short, spiniform seta; posterior margin sparsely setose (Fig. 27). . . . . ***Biffarius cf. fragilis*** (Biffar, 1970)

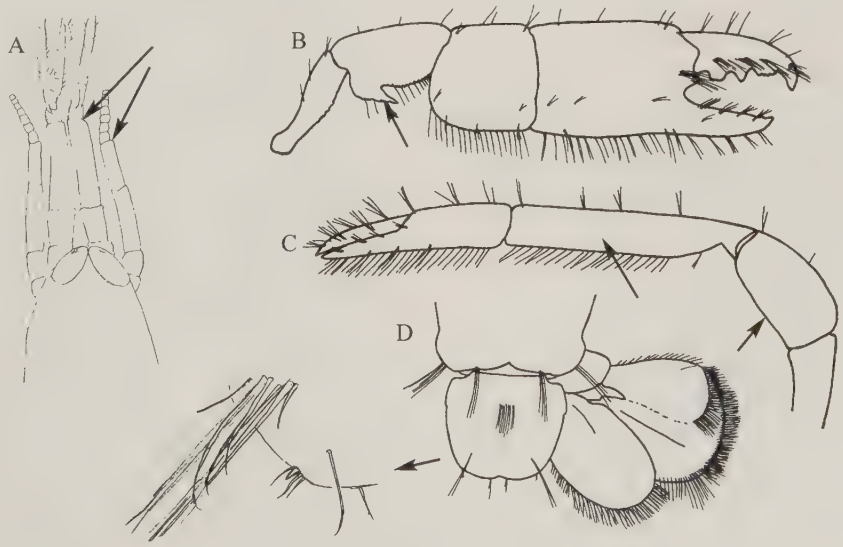


**Figure 27**

*Biffarius cf. fragilis*: (A) dorsal view of anterior carapace; (B) pereopod 1 major chela; (C) pereopod 1 minor chela; (D) telson and uropods, with enlargement of posterolateral corner of telson. A and enlargement of telson: original illustrations by R. W. Heard; B–D modified from Biffar, 1971b.

## Synopsis of Thalassinidea known from the South Atlantic Bight

### INFRAORDER THALASSINIDEA Latreille, 1831

#### SUPERFAMILY AXIOIDEA Huxley, 1879

##### Family Axiidae Huxley, 1879

*Acanthaxius* Sakai and de Saint Laurent, 1989
***Acanthaxius hirsutimanus*** (Boesch and Smalley, 1972)
(Fig. 10)

*Calocaris (Calastacus) hirsutimana* Boesch and Smalley, 1972: 45–52.

*Axiopsis hirsutimana.*—Williams, 1984: 187.

*Acanthaxius hirsutimanus.*—Sakai and de Saint Laurent, 1989: 73.

**Material examined.** SERTC #S780, one female, off Tybee Island, GA, 32°00.0′N, 80°11.6′W, 137 m, coll. MARMAP, 5 April 1975. ULLZ #1474, one female, 40 miles SSW of Grand Isle, LA, 40 fathoms, coll. D.L. Felder, July 1975, identification by D.L. Felder.

**Diagnosis.** (Modified from Boesch and Smalley, 1972.) Carapace with five gastric carinae (one medial, two submedial, and two lateral); medial carina with eight spines; submedial carinae with five spines; lateral carinae with six or seven spines; medial carina continues posteriorly for length of carapace after short trench extending from cervical groove. Eyes with eyestalks well developed and overreaching rostrum. First pereopods (chelae) unequal in size, robust, heavily setose. Uropodal exopods broad, sub equal in length to telson.

**Known range.** Gulf of Mexico, tropical Atlantic, off Guyana, Costa Rica (Boesch and Smalley, 1972; Vargas and Cortés, 1999), South Atlantic Bight (Wenner and Read, 1982), off Santee Rivers, SC (Wenner et al., 1984), off Kiawah Island, SC (Wenner et al., 1984), off Tybee Island, GA (present study).

**Habitat.** Soft bottom substrata, 11 to 137 m.

**Remarks.** This species was originally described based on specimens from off northeastern South America and the northeast Gulf of Mexico (Boesch and Smalley, 1972). The first SAB record of the species was reported by Wenner and Read (1982) in a study of the shelf and upper slope Crustacea. During the present investigation a single female specimen was found in the marine invertebrate collection of the College of Charleston's Grice Marine Laboratory (GML) from off Tybee Island, Georgia.

There appear to be distinctive differences, especially in size, shape, and ornamentation of the first pair of chelae, between the specimen of *A. hirsutimanus* from Georgia and the original description. These differences could be ecophenotypic, the result of re-growth after the individual was damaged, or representative of specific differences. Further study of additional material is needed before any conclusions can be made.

*Axius* Leach, 1815
***Axius armatus*** S. I. Smith, 1881
(Fig. 15)

*Axius armatus* S. I. Smith 1881: 433.

**Material examined.** SERTC #S783, two females, off St. Helena, SC, 31°41′N, 79°25′W, 232 m, coll. *R/V Dolphin*, 21 September 1976. USNM 174450, one ovig. female, off South Carolina, 32°30′N, 78°29′W, Sta. 2G, 218 m, coll. by Texas Instruments, Inc. for BLM/MMS, SABP, 20 November 1977. USNM 174451, one male, off South Carolina, 32°30′N, 78°29′W, Sta. 2G, 218 m, box corer, coll. by Texas Instruments, Inc. BLM/MMS, SABP, 12 May 1977.

**Diagnosis.** (Modified from Kensley, 2001.) Carapace with submedial carina unarmed, without supraocular spines. Rostrum longer than eyes, with 3–6 pairs of spines along lateral edges. Antenna 2 with scaphocerite well developed, simple. Pereopod 1 major chela fixed finger of propodus with single spine; merus armed with 3–4 ventral spines, dorsal margin strongly carinate; minor chela lacking spine on fixed finger of propodus; merus dorsal margin with single spine, ventral margin with 4 spines. Pereopod 2 merus ventral margin setose, with 4 spines. Pereopod 4 sternal plate with lateral flange rounded. Telson with 4–6 dorsal spines at mid length. Uropodal exopod transverse suture armed with 7–8 spines.

**Known range.** U.S. Atlantic Seaboard from Massachusetts to South Carolina (Kensley, 2001; present study).

**Habitat**. Continental shelf, 108–260 m.

**Remarks.** Prior to this report, this species was known from only two records in the SAB from off the coast of South Carolina (Kensley, 2001). There are few records of this species in the literature, all of which are female (Kensley, 2001). Two specimens from off St. Helena, SC examined in this study (SERTC S#783) represent the third report of this species in the SAB.

*Axius armatus* appears to be primarily a resident of the waters off the northeast U.S. coast (Kensley, 2001). In the northern portions of its range, it is sympatric

with the morphologically similar and apparently closely related species *Axius serratus* Stimpson, 1852. For more information on these two species refer to Kensley (2001).

***Calaxius*** Sakai and de Saint Laurent, 1989
***Calaxius jenneri*** (Williams, 1974)
(Fig. 12)

*Calocaris (Calastacus) jenneri* Williams, 1974: 451.
*Axiopsis jenneri.*—Williams, 1984: 185.
*Calaxius jenneri.*—Sakai and de Saint Laurent, 1989: 86.

**Material examined.** SERTC #S778, 10 specimens, off Charleston, SC, 32°06.5′N, 79°12.5′W, 79 m, coll. by GML staff, 23 April 1977, housed within the College of Charleston's Grice Marine Laboratory marine invertebrate collection. USNM 174448, one male specimen, off Sapelo Island, GA, 30°57.08′N, 79°57.85′W, 62 m, coll. by Texas Instruments, Inc. for BLM/MMS, SABP, 30 August 1977. USNM 214904, one specimen, off Savannah, GA, 31°32.0′N, 79°44.4′W, 56 m, coll. by South Carolina Marine Resources for BLM/MMS, R/V Oregon, Sta. OS01, fly net, 10 March 1981.

**Diagnosis.** (Modified from Williams, 1974.) Carapace nearly smooth, with scattered tufts of setae; lateral carinae with a small spine, sub medial carinae with four spines. Rostrum acute, extending slightly beyond eyes; tip slightly upturned with 1–3 spines on lateral margins. Eyes with cyclindrical stalks; cornea rounded, well developed, pigmented. Antenna 2 with scaphocerite long and slender. First pereopods (major and minor) sub equal, asymmetrical, densely setose. Major chela strongly developed, fingers with distinct gap proximally; propodus (including fixed finger) about same length as carapace, fixed finger with spine; dactylus (movable finger) with distally inflated cutting edge. Telson rounded posteriorly; posterior margin fringed with setae, lacking posterio-medial spine. Uropodal exopod with transverse distal suture with short, stout spines.

**Known range.** Southwest of Cape Lookout, NC (Williams, 1974), South Atlantic Bight (Wenner and Read, 1982), and off Savannah River, GA (Wenner et al., 1984, as *Axiopsis hirsutimana*; present study).

**Habitat.** Deep continental shelf and upper slope, 62 to 232 m (Williams, 1974; Wenner and Read, 1982; present study).

**Remarks.** This species was transferred to the new genus *Calaxius* by Sakai and de St. Laurent (1989), which then contained eight species. Kensley and Hickman (2001) subsequently recognized 10 species and divided the genus into two groups: species "with strongly triangular and ventrally acute abdominal pleura," and "those with ventrally rounded pleura." Felder and Kensley (2004) added an eleventh species to this genus based on material from chemosynthetic (seep) communities off the Louisiana continental slope.

This species was previously recorded in the literature solely from North Carolina (Williams, 1974; Williams, 1984). Wenner and Read (1982) recorded two specimens from 232 m in the South Atlantic Bight that they identified as "*Calocaris jenneri*" but we have been unable to locate the material to confirm the identification. Wenner et al. (1984) recorded one specimen of "*Axiopsis hirsutimana*" from 56 m, near the shelf edge off Savannah, Georgia, that we found in the USNM collections (USNM 214904) and re-identified as *Calaxius jenneri*. In our examination, 10 additional specimens from South Carolina of *C. jenneri* were located in the collections of the GML.

***Paraxiopsis*** De Man, 1905
***Paraxiopsis gracilimana*** Kensley, 1996
(Fig. 14)

*Paraxiopsis gracilimana* Kensley, 1996: 719–722, figs. 6, 7.

**Material examined.** USNM 169669 (Holotype), female, Bonaire Harbor, Netherlands Antilles, 2 m, coll. *R/V Harrison*, 25 August 1976. USNM 211454 (Paratypes) one female, one juvenile, Looe Key Reef, FL, sta FLK-21, 6 m, coll. B. Kensley and M. Schotte, 29 September 1982. USNM 174452, off South Carolina, 3245N, 7856W, Sta 2D, 27 m, coll. by Texas Instruments, Inc. for BLM/MMS, SABP, 25 August 1977.

**Diagnosis.** (Modified from Kensley, 1996.) Carapace with surface smooth, lateral carina more or less continuous with lateral rostral margin, armed with a single pair of anterior spines, submedial carina with a single pair of anterior spines, medial carina lacking spines; rostrum extending beyond eyes, with four pairs of lateral spines (each with associated seta) that get progressively smaller (in smaller specimens there may also be 1–2 pairs of very small spines towards the rostrum tip). Abdominal pleura ventrally rounded, with small spine on anterior margin of pleura 3–5. Telson lateral margins with four pairs of spines and a pair of distal robust setae, dorsal surface with three pairs of spines, distal margin with small medial spine.

**Known range.** South Carolina southward and westward to Gulf of Mexico; throughout Caribbean as far south as Tobago (Kensley, 1996).

**Habitat.** Live bottom habitats, 1 to 27 m (Kensley, 1996).

**Remarks.** This species is known in the SAB from a single record off South Carolina (Kensley, 1996). Examination of the South Carolina specimen led to questions regarding the rostrum and maxilliped morphology that could not be answered in Kensley's (1996) description and it was apparent that the types for this species would need to be examined. Subsequently, it was found that smaller specimens have 1–2 pairs of much smaller spines on the anterior portion of the rostrum, in addition to the four pairs of spines described. Also, on maxilliped 3 the mesial edge of the merus possesses around 17 spines along its entire length. While the spines on the mesial edge of maxilliped 3 were not illustrated by Kensley (1996), it was given as a general diagnostic character for the genus.

*Paraxiopsis gracilimana* is the type-host for the bopyrid isopod, *Gigantione uberlackerae* Adkison, the type locality of which is the northern Gulf of Mexico (Adkison, 1984). At present this isopod parasite is not known from the SAB.

### Family Calocarididae Ortmann, 1891

***Calocaris*** Bell, 1853
***Calocaris templemani*** Squires, 1965
(Fig. 8)

*Calocaris templemani* Squires, 1965: 2, figs. 1, 2A, 2B, CtC, CtD, 3Ct, 4, 5Ct, 6.

**Material examined.** USNM 294422, one female, off Cape Lookout, NC, 34°14.86′N, 075°43.78′W, 1013 m, *R/V Columbus Iselin*, coll. by Battelle New England Marine Lab. for BLM/MMS, ASLAR, Sta. SA1:02, box corer, Core 7, 12 Nov 1983.

**Diagnosis.** (Modified from Williams, 1984.) Carapace having medial carina extending full length, continuing on to rostrum. Eyes with pigment indistinct (diffuse or appearing absent), eyestalk rudimentary, flattened obliquely on distal surface. Antenna 2 peduncular article 2 with small lateral spine and lateral scale reduced to a short spine. Telson rounded distally, lateral margin with a small pair of anterior spines. Uropodal exopod with a weakly defined, partially fused distal suture, suture lacking spines.

**Known range.** Newfoundland to Virginia; off Cape Lookout, NC (Squires, 1965; Williams, 1984).

**Habitat.** Soft sediments, 200–1013 m (Williams, 1984).

**Remarks.** Although the single specimen from off Cape Lookout represents the known southern limit for this species, it is possible that this species occurs in deeper waters further south (Williams, 1984).

## SUPERFAMILY CALLIANASSOIDEA Dana, 1852

### Family Callianassidae Dana, 1852

### Subfamily Callianassinae Dana, 1852

***Biffarius*** Manning and Felder, 1991a
***Biffarius biformis*** (Biffar, 1971a)
(Fig. 26)

*Callianassa biformis* Biffar, 1971a: 225, fig. 1.
*Biffarius biformis.*—Manning and Felder, 1991a: 769.

**Material examined.** SERTC #S777, one male, six females, Edisto Beach, near entrance to Big Bay Creek, SC, 32°29.6′N, 80°20.7′W, intertidal, coll. by GML staff, 20 August 1972. SERTC #S1072, one male, one ovigerous female, two undetermined, on protected beach near Cummings Point, Morris Island, SC, 32°44.48′N, 79°52.38′W, intertidal, coll. By R. Heard, 13 May 2004. USNM 42401 (labeled as *Gilvossius setimanus*) off Beaufort, NC. USNM 150246, two female, three males, Sapelo Island Beach, GA, intertidal, coll. by M. Gray, 9 February 1961. USNM 155371, 10 females, 16 males, south end of Sapelo Island, GA, intertidal, coll. by R. Heard, 6 April 1969. USNM 266218, 50+ males and females, north end of Saint Catherines Island, GA, intertidal, coll. by GA Bishop, yabby pump, 1 June 1988.

**Diagnosis.** (Modified from Biffar, 1971a.) Antenna 1 peduncle shorter than antenna 2 peduncle. Eyes flattened proximally, rounded distally, cornea central; eyestalks shorter than first antennular segment. In males, the first pair of chelae are greatly unequal in size, with two forms of major chelae (a "strong" form and a "weak" form); ischium dorsal margin with small spur-like projection; merus dorsal margin with fringe of setae, ventral margin with hook-like projection. In females, the first pair of chelae are more or less symmetrical, resembling the minor chela of the male, not noticeably elongate; merus ventral margin with small curved hook-like projection; carpus narrower than propodus, length about three times greatest width. Telson distal margin bluntly rounded and lacking medial projection, lateral margins each with pair of small distal spiniform setae present. Uropodal exopod irregularly shaped, basically bilobed distally; endopod rounded.

**Known range.** Massachusetts to Georgia (Sapelo Island); northern Gulf of Mexico, including Bald Point, Franklin County, FL; Louisiana, Corpus Christi, TX, and the south Texas outer continental shelf (Biffar, 1971a; Rabalais et al., 1981).

**Habitat.** Lower intertidal in the vicinity of the mouths of sounds, bays, and inlets to about 10 m depths offshore in fine to moderate sand and sand-silt substrata; salinity 10–30‰ (Biffar, 1971a).

**Remarks.** In the SAB, *Biffarius biformis* has been reported from both lower intertidal (Biffar, 1971a) and subtidal habitats (Dörges, 1972, 1977; Frankenberg and Lieper, 1977; Prezant et al., 2002; Van Dolah et al.[1]; Jutte and Van Dolah[2]; Jutte et al.[3]; Van Dolah et al.[4]). In past studies this species has been confused with juveniles of *C. atlantica* (=*Gilvossius setimanus*) (Frey and Howard, 1969; Biffar, 1971a). Populations are known to occur seaward to depths of 7–8 m over 3 km off the mouth of Doboy Sound, Georgia (Smith, 1971). Dörges (1977) considered it one of the dominant organisms in high salinity estuaries and the inner shelf outside the wave zone in Georgia. One population with densities exceeding 50 individuals per $m^2$ was discovered on the north shore of Tybee Inlet, near the mouth on the south end of Tybee Island, Georgia (Heard, pers. observ.). See Frey and Howard (1969) for a description of *B. biformis* burrows.

*Biffarius biformis* has been reported off the Texas coast in depths of 10–15 m (Rabalais et al., 1981); however, the specific status of the Texas and other northern Gulf of Mexico populations needs to be verified by analysis of morphological and molecular data (Felder[5]).

[1] Van Dolah, R. F., R. M. Martore, A. E. Lynch, M. V. Levisen, P. H. Wendt, D. J. Whitaker, and W. D. Anderson. 1994. Environmental evaluation of the Folly Beach nourishment project. Final Report to the U.S. Army Corps of Engineers, Charleston District. Charleston, SC. 100 p. and appendices. Marine Resources Research Institute, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

[2] Jutte, P. C., and R. F. Van Dolah. 1999. An assessment of benthic infaunal assemblages and sediments in the Joiner Bank and Gaskins Banks borrow areas for the Hilton Head beach renourishment project. Final Report – Year 1 to Olsen Associates, Inc. and the Town of Hilton Head Island from the Marine Resources Division, South Carolina Department of Natural Resources. 33 p. Marine Resources Research Institute, South Carolina Department of Natural Resources, PO Box 12559, Charleston, SC 29422.

[3] Jutte, P. C., R. F. Van Dolah, G. W. Eason, Jr., and M. V. Levisen. 1999. An assessment of benthic infaunal assemblages and sediments in the vicinity of the Port Royal Ocean Dredged Material Disposal Site. Final Report to the U. S. Army Corps of Engineers, Charleston District. Charleston, SC. 55 p. Marine Resources Research Institute, South Carolina Department of Natural Resources, PO Box 12559, Charleston, SC 29422.

[4] Van Dolah, R. F., P. C. Jutte, G. H. M. Riekirk, M. V. Levisen, L. E. Zimmerman, J. D. Jones, A. J. Lewitus, D. E. Chestnut, W. McDermott, D. Bearden, G. I. Scott, and M. H. Fulton. 2002. The condition of South Carolina's estuarine and coastal habitats during 1999–2000: Technical Report No. 90. South Carolina Marine Resources Division. 132 p. Marine Resources Research Institute, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

[5] Felder, D. Pers. commun. University of Louisiana at Lafayette, Department of Biology, PO Box 42451, Lafayette, LA 70504.

***Biffarius* cf. *fragilis*** (Biffar, 1970)
(Fig. 27)

*?Callianassa fragilis* Biffar, 1970: 45, fig. 3.
*?Biffarius fragilis.*—Manning and Felder, 1991a: 769.

**Material examined.** USNM 174404, 1 male, off South Carolina, 32°54.1′N, 79°11.98′W, 17 m, TI/MMS, Sta. 2B, 17 November 1977.

**Diagnosis.** (Modified from Biffar, 1970.) Eyestalks with apices rounded (lacking acute, elongate tips). Antenna 1 peduncle equal to or extending slightly beyond antenna 2 peducle. Third maxilliped with ischium and merus subquadrate, longer than wide. Major chela of male and female with hook-like projection on inner margin of merus; major chela of male much larger and strongly developed (nearly as long as entire body) than that of female. Minor chelae of both male and female similar, distinctly elongate with merus lacking hook-like spine; carpus narrow, 5–6 times greatest width. Pleopods 3–5 having short stubby-like appendices internae. Telson lacking distinct medial grove, each posterior lateral corner with single, short, spiniform seta; posterior margin sparsely setose, lacking medial projection. Uropodal endopod rounded, length less that two times width.

**Known range.** South Carolina; Florida; Puerto Rico; Antigua; Venezuela (Biffar 1970, 1971b; present study).

**Habitat.** Intertidal to shallow subtidal; sand, clay or mud substrates (Biffar, 1970).

**Remarks.** The single damaged specimen from South Carolina is similar in most respects to the description of the species given by Biffar (1970, 1971b); however, it differs slightly in the dentition of the cutting edges of the major chela and the presence of a single, short spiniform seta on each posterior lateral margin of the telson. The presence of this spiniform seta was not noted by Biffar (1970, 1971b) and may represent a variable characters or evidence for a yet undescribed species.

***Gilvossius*** Manning and Felder, 1991b
***Gilvossius setimanus*** (DeKay, 1844)
(Fig. 24)

*Gonodactylus setimanus* DeKay, 1844: 34.
*Callianassa stimpsoni* S. I. Smith, 1873: 549, pl. 2, fig. 8.
*Callianassa atlantica* Rathbun, 1926: 107.
*Callianassa setimanus.*—Manning, 1987: 388.
*Gilvossius setimanus.*—Manning and Felder, 1991b: 558.

**Material examined.** USNM 51007, fishing grounds off Beaufort, NC, 34°22′N, 076°57′W, 29 m, *R/V Fish Hawk*, Sta. 7958, 7 Sept. 1913. USNM 174405, off South Carolina, 32°57.0′N, 79°17.0′W, 12.5 m, coll. by Texas Instruments, Inc. for BLM/MMS, SABP, Sta. 2A, box corer, 12 February 1977. USNM 68386, one female, Wassaw Sound, Cabbage Island, Chatham County, GA, coll. by I. R. Tomkins, 01 April 1933.

**Diagnosis.** (Modified from Williams, 1984.) Antennular peduncle extending beyond distal tip of antenna 2 peduncle. Eye with cornea laterally positioned; eyestalks extending beyond first antennular segment, narrowing distally and curving outward. Pereopod 1 chelae unequal and showing sexual dimorphism; major chela merus ventral margin with strong hook-like projection in males (smaller in females); minor chela with carpus about as wide as propodus merus, ventral margin entire. Telson posterior margin bluntly rounded, with small medial spine. Uropodal exopod distally rounded, two distinct areas defined on dorsal surface by distal fringes; endopod distally rounded.

**Known range.** Nova Scotia to southern Georgia (Williams, 1984; Manning, 1987).

**Habitat.** Lower intertidal and shallow subtidal to depths of 134 m, firm mud-sand substrates, salinity 25–32‰ (Frankenberg and Leiper, 1977; Rabalais et al., 1981; Williams, 1984; Van Dolah et al.[6]). Deeper records of "*Callianassa atlantica*" have been recorded within the South Atlantic Bight (collected at 218 m and 401 m and recorded by Tenore[7] in the South Atlantic Benchmark Program 1977 Report) (Knott and Wendt[8]). Despite our efforts, we have not been able to locate these specimens for examination, therefore the maximum depth record for this species within the South Atlantic Bight remains at 134 m.

**Remarks.** Individuals of this species are intermediate in body length (59 mm males, 68 mm females) between *Callichirus major* (Say, 1818) (95 mm males, 80–92 mm females) and the smaller *Biffarius biformis* (32 mm males, 27 mm females). *Gilvossius setimanus* is easily distinguished from the superficially similar *B. biformis* by the shape of the third maxilliped, the tail fan, and the outwardly curved apices of the eyestalks. *Gilvossius setimanus* has been collected irregularly and may be more characteristically found subtidally in the higher salinity waters of the sounds and bays of the SAB; however, a well-established intertidal population was present on an exposed mud-sand bar with associated oysters on the Bull River side of Cabbage Island, Wassaw Sound, Georgia (Heard, pers. observ.).

During September and October of 1968, specimens were found in the stomachs of large specimens of the Atlantic stingray *Dasyatis sabina* (Lesueur) near the mouth of St. Catherines Sound (Heard, pers. observ.). An additional adult specimen was also found in the stomach of a large American stingray, *D. americana* Hildebrand and Schroeder, in the mouth of Calibogue Sound, South Carolina (Heard, pers. observ.). The species has also been found to be occasional prey of tomtate, *Haemulon aurolineatum* Cuvier 1830, and whitebone porgy, *Calamus leucosteus* Jordan and Gilbert 1885, in studies of food habits of fish on the continental shelf between Santee River, South Carolina and Jacksonville, Florida (MRRI)[9].

The bopyrid isopod, *Ione thompsoni* Richardson, 1904, was originally described from the branchial chamber of *G. setimanus* in New England (Markham, 1995). This isopod parasite was found on specimens of *G. setimanus* collected in the lower intertidal zone of Cabbage Island (Wassaw Sound), Georgia (Heard, pers. observ.) and it was found infesting this host in an intertidal area just south of St. Augustine, Florida (Maturo[10]).

***Necallianassa*** Heard and Manning, 1998
***Necallianassa berylae*** Heard and Manning, 1998
(Fig. 20)

*Necallianassa berylae* Heard and Manning, 1998: 884.

**Material examined.** USNM 260881 (Holotype), one male, off South Carolina, 32°00.95′N, 79°31.05′W, 43 m, TI/MMS Pierce Sta. 9737, sample 0177-2 (3E), August 1977. USNM 260882 (Paratype), one female,

[6] Van Dolah R. F., D. R. Calder, D. M. Knott, and M. S. Maclin. 1979. Effects of dredging and unconfined disposal of dredged material on macrobenthic communities in Sewee Bay, South Carolina. South Carolina Marine Resources Center Technical Report 39. 54 p. Marine Resources Research Institute, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

[7] Tenore, K. R. 1978. Macroinfaunal benthos. *In* South Atlantic Benchmark Program 1977 Report, Volume 3, p. 255–288 and appendices. Prepared for the Bureau of Land Management, Outer Continental Shelf Office, New Orleans, LA by Texas Instruments, Inc., Dallas, TX, 440 p.

[8] Knott D. M., and P. H. Wendt. 1985. Special literature analysis study: Final report on benthic communities in certain slope areas of the South Atlantic Bight. Prepared for Minerals Management Service, Washington, D.C., Contract 14-12-0001-29185, OCS study MMS 85-0051, 75 p. Marine Resources Research Institute, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

[9] Marine Resources Research Institute. 1984. Final Report, South Atlantic OCS Area Living Marine Resources Study, Phase III. Vol. II: Appendices. Prepared for Minerals Management Service, Washington, D. C., Contract 14-12-0001-29185. 82 p. Marine Resources Research Institute, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

[10] Maturo, F. J. S. 2006. Pers. commun. University of Florida, Box 118525, Gainesville, FL 32611-8525.

off South Carolina, 32°00.95′N, 79°31.05′W, 43 m, TI/MMS Pierce Sta. 9737, sample 0177-2 (3E), August 1977. USNM 260886 (Paratype), off Georgia, 31°33.63′N, 79°39.02′W, 75 m, 6 August 1963. USNM 260887 (Paratype), off Georgia, 31°33.06′N, 79°40.35′W, 65 m, 6 August 1963. USNM 260888 (Paratype), off Georgia, 31°33.05′N, 79°40.63′W, 53 m, 6 August 1963. USNM 174408, one specimen, off North Carolina, 32°12.00′N, 77°36.00′W, 44 m, TI/MMS Sta. 1E, 10 May 1977; USNM 174411, one specimen, off South Carolina, 31°27.00′N, 79°46.00′W, 64 m, TI/MMS Sta. 4F, 28 August 1977.

**Diagnosis.** (Modified from Heard and Manning, 1998.) Rostrum acute, sharp, reaching about ¾ the length of the eyestalks. Eyestalks dorso-ventrally flattened. Pereopod 1 chelae sexually dimorphic; major chela of males with ischium narrow, ventral margin crenulate; merus ventral margin with hook-like projection (projection smaller in females). Telson lateral margins with 1–2 pairs of spines, distal margin with medial spine. Uropodal endopod with lateral spine.

**Known range.** Georgia, North Carolina, and South Carolina (Heard and Manning, 1998).

**Habitat.** Sub tidal soft sand substrata, depths of 35 to 75 m (Heard and Manning, 1998).

**Remarks.** The species was described by Heard and Manning (1998) based on material from off Georgia and South Carolina. This species appears to be the western Atlantic cognate of *Callianassa acanthura* Caroli, from the eastern Atlantic waters of the Mediterranean. At the time *N. berylae* was described, two eastern Atlantic species were transferred to *Necallianassa*: *Callianassa acanthura* Caroli, 1946 and *C. truncata* Giard and Bonnier, 1890. However, in 1999, Sakai synonymized *Necallianassa* with *Callianassa*. Ngoc-Ho (2003) re-examined the group and declared *Necallianassa* a valid monotypic genus, containing only *N. berylae*, based on the large rostral spine, the lateral spines on the telson, the morphology of the uropods, and female with pleopod 2 lacking an *appendix interna*. We follow Ngoc-Ho (2003), in accepting *Necallianassa* as a valid genus.

### Subfamily Callichirinae Manning and Felder, 1991a

**Genus *Callichirus*** Stimpson, 1866
***Callichirus major*** (Say, 1818)
(Fig. 22)

*Callianassa major* Say, 1818: 238.
*Callichirus major*.—Hay and Shore, 1918: 407, pl. 29, fig. 10.

**Material examined.** SERTC #S779, one specimen, Folly Beach, Charleston, SC, 32°41.5′N, 79°53.4′W, intertidal, coll. by GML staff, 1 August 1985. SERTC #S1969, six males, five females, Folly Beach, Charleston, SC, 32°38.49′N, 79°57.91′W, intertidal, coll. by SERTC staff, March 2005. USNM 78348, one female, one male, Edisto Beach, SC, coll. by H. G. Rutledge, 3 August 1937. USNM 150248, two females, Sapelo Island Beach, GA, intertidal, coll. by M. Gray, 20 November 1961. USNM 266228, 45 females, 5 males, north beach of Saint Catherines Island, Georgia, intertidal, coll. by G. A. Bishop, yabby pump, 1988.

**Diagnosis.** (Modified from Williams, 1984.) Rostrum minute. Eyes with cornea reduced, near middle of lateral margin of ocular peduncles. Antennular peduncles approximately ⅔ as long as carapace, densely setose ventrally, terminating in two sub equal flagella. Chelae unequal, sexual dimorphism present; in major chela of males ischium and merus ventral margins granular; merus with ventral spine; carpus proximal ventral margin granular, dactylus hooked over fixed finger of propodus and with a proximal granular process on the ventral margin; the ischium, merus, and carpus ventral margins are smooth; merus does not have process on ventral margin uropods and telson lacking lateral processes; uropodal endopod narrow (approximately four times long as wide), with only terminal setae.

**Known range.** Cape Lookout, North Carolina southward to Florida, the Gulf of Mexico; northern South America (Williams, 1984; Heard, pers. observ.).

**Habitat.** In the SAB this species occurs on open beaches, primarily in the intertidal zone (Dörges, 1972; Kirby-Smith and Gray, 1977; Prezant et al., 2002) but also in shallow subtidal depths (2–3 m). It occurs in salinities ranging from 15–36‰ and can tolerate salinities as low as 10‰ for short periods. It constructs deep burrows with some approaching depths of 2 m (Weimer and Hoyt, 1964; Heard, pers. observ.).

**Remarks.** This large callianassid is one of the most common, characteristic and bionomically important species on the open beaches of the SAB, but because it occurs in deep burrows *C. major* is seldom observed or collected. As with all callianassids, it is a permanent burrow dweller with the only indication of its presence being a small hole fringed with fecal pellets. Ovigerous females were observed in June and July near Beaufort, South Carolina (Pearse et al., 1942) and in August on Sapelo Island, Georgia (Heard, pers. observ.). The burrow morphology on Sapelo Island and surrounding areas have been studied and described by Weimer and Hoyt (1964) as tube shaped, from 1 to 2 meters

in depth, with walls ¼ of an inch thick, and bound together by a brown cementing agent consisting of callophanite (amorphous calcium phosphate). The fecal pellets of this organism were used in studies of the biological significance of coprophagy in estuarine animals by Frankenberg et al. (1967) and Frankenberg and Smith (1967).

Two commensal crustaceans are often associated with *C. major*, a bright orange copepod, *Clausidium dissimile* Wilson, 1921, which is found on the body surface, branchial cavity, and burrow wall; and a small elongate, pinnotherid crab *Austinixa cristata* (Rathbun), which occurs in the upper constricted part of the burrows (Williams, 1984; Heard, pers. observ.). The larval stage of the tapeworm *Prochristianella hispida* (Linton, 1890) occurs in the digestive gland of *C. major* where its oval-shaped whitish-colored blastocysts can often be observed through the translucent exoskeleton of its host. The adult stage of this marine tapeworm matures in the spiral valve of the blunt nose stingray, *Dasyatis sayi* (Lesueur), which represents one of the few predators capable of extracting the *C. major* host from its burrows (Overstreet, 1983; Heard, pers. observ.).

### Subfamily Cheraminae Manning and Felder, 1991a

***Cheramus marginatus*** (Rathbun, 1901)
(Fig. 18)

*Callianassa marginata* Rathbun, 1901: 92, fig 15.—Borradaile, 1903: 547.—Biffar, 1971b: 689–694, figs 15, 16.
*Cheramus marginatus*.—Manning and Felder, 1991a: 780, fig. 14.

**Material examined.** USNM 174406, one ovigerous female, off the coast of Georgia, 30°53.98′N, 79°43.96′W, 383 m, coll. by TI/MMS, 17 May 1977, Id by: B. Boothe. USNM 174407, one specimen, off Florida, 29°35.98′N, 80°11.00′W, 241 m, coll. by TI/MMS, Sta.7E, 20 May 1977.

**Diagnosis.** (Modified from Manning and Felder, 1991a.) Rostrum acute, reaching beyond eyes. Eyes with cornea lateral, subterminal. Pereopod 1 major chela ischium inner margin with short spines; merus with inner margin unarmed. Pleopods 3–5 with finger-like appendices internae. Telson distal margin bilobed, with medial spine, with 3 robust seta on the distolateral margins. Uropodal exopod subquadrate, more than twice as long as wide and nearly twice as long as telson.

**Known range.** Puerto Rico, Mexico, Texas, southeast Florida and Georgia (Rathbun, 1901; Biffar, 1971b; present study).

**Habitat.** Soft substrata on the deep shelf and upper slope, 40 to 383 m.

**Remarks.** This species was originally described as *Callianassa marginata* by Rathbun (1901) based on specimens from Puerto Rico, from depths of 40 m to more than 314 m (Rathbun, 1901). In 1991, Manning and Felder transferred this species to the genus *Cheramus* Bate, 1888.

Confirmation of the presence of this species within the SAB has been elusive. Biffar (1971b) reported the species from off Miami Beach. Abele and Kim (1986) included the species (as *Callianassa marginata*) in their illustrated key to the marine decapod crustaceans of Florida, but did not indicate the species distribution. The two specimens examined from the USNM collections constitute a documented range extension of the species.

We compared the ovigerous female from off Georgia with specimens collected off Puerto Rico, which were made available to us by Barry A. Vittor & Associates (SERTC #S2805). Several differences were observed including (1) differences in type, size, and number of setae on the uropods and telson, (2) the shape and length/width ratios of the uropodal endopods and exopods, and (3) the shape and dentition of the chelae. One of the more distinctive differences was the length/width ratios of the uropodal exopods (Georgia length/width: 1.8 vs. Puerto Rico length/width: 2.5). Whether or not these differences are clinal or indicate the possibility of a cryptic species being present in the SAB can only be resolved by study of additional specimens from the waters off Georgia and possibly the Carolinas.

### Family Laomediidae Borradaile, 1903

***Naushonia*** Kingsley, 1897
***Naushonia crangonoides*** Kingsley, 1897
(Fig. 2)

*Naushonia crangonoides* Kingsley, 1897: 96, pl. 3, figs. 8–10.—Goy and Provenzano, 1979: 339–359, figs 1–8.

**Material examined.** USNM 170634, one male, two females, off Cobb Island, Virginia, 37°15′N, 075°40′W, 14 m, Sta. 66, *R/V Delaware II*, trawl, 2 October 1977.

**Diagnosis.** (Modified from Williams, 1984.) Carapace cylindrical. Rostrum flattened, broadly rounded. Eyes not visible from above; pigment reduced. First leg strongly subchelate; dactyl articulated to fold back against the distoventral margin of the elongate palm. Second leg simple, not chelate. Uropod with distinct suture on both endopod and exopod. Telson broadly rounded.

**Known range.** Newfoundland to Gulf of Maine; off Cape Lookout, NC (Williams, 1984).

**Habitat.** Soft bottom in sand and mud, near shore to 14 m (Williams, 1984).

**Remarks.** This species is represented in the SAB by a single post-larva collected from Bogue Sound in North Carolina in a surface plankton sample identified by Williams (1984). The present authors did not examine this specimen; nonetheless the species is included within this guide given that it may be present in the northern region of the SAB.

### Family Thomassiniidae de Saint Laurent, 1979

*Crosniera wennerae* Heard and King, 2007
(Fig. 16)

**Material examined.** USNM 174403, one male, off North Carolina, 33°00.96′N, 77°20.20′W, 318 m, TI/MMS Station 1F, 10 February 1977.

**Diagnosis.** (Modified from Heard and King, 2007.) Female: Carapace with *linea thalassinica* not extending into posterior half; rostrum short, acutely tipped, extending to, or just short of tips of eyes. Eye stalks with subacute tip, dorsally rounded and flattened ventrally; eyes poorly developed, each with two ommatidia and some defuse pigment. Maxilla 2 posterior lobe of scaphognathite bearing single long distinctive seta. Maxilliped 2 and 3 each with well-developed exopod, extending beyond articulation of merus and propodus. Maxilliped 3 lacking spine on distal, flexor margin of merus. Pereopod 1 (first chelae) sub equal (left chela slightly more robust); merus lower margin convex, smooth except for few small simple setae; left (major) chela with cutting edge of fixed finger bearing strong blunt subdistal spine and small proximal spine near articulation with movable finger; right (minor) chela with fixed finger having single, relatively small, low spine midway along cutting edge. Pereopod 3 with propodus having distal margin armed with single spiniform seta. Uropods broadly rounded; exopod not bilobed, entire (no lateral spine). Telson dorsal surface smooth with shallow lobes proximally on each margin, posterior margin broadly rounded and fringed with plumose setae.

**Known range.** Collected from off North Carolina.

**Habitat.** The single nonovigerous female specimen was obtained at a depth of 318 m in soft substratum on the continental slope.

**Remarks.** *Crosniera wennerae* is distinguished from the other four nominal species of the genus by having maxillipeds 2 and 3 with relatively long exopods that extend well past the merus of the endopod. It appears to have closer affinities with *C. corindon* Poore, 1997, a western Pacific species known only from Indonesia (Poore, 1997), than with *C. minima,* the only other member of the genus currently known from the western Atlantic. *Crosniera wennerae* differs from *C. minima* in several characters, including: (1) the shape and dentition of the first chelae, (2) the absence of a lateral spine on both the uropodal endopod and exopod, (3) the absence of one or two submarginal, elongate, spiniform setae near distal margin of each uropodal endopod, and (4) the absence of lateral spines on the margins of the telson.

### Family Upogebiidae Borradaile, 1903

*Upogebia* Leach, 1814
*Upogebia affinis* (Say, 1818)
(Fig. 6)

*Gebia affinis* Say, 1818: 241.
*Upogebia affinis.*—Stebbing, 1893: 185.

**Material examined.** SERTC #S611, two females, Southern Bass Hole Bay, north of Cooks Creek, SC, intertidal, coll. by GML staff, 13 September 1970. SERTC #S776, seven specimens, tide pool, on west side of Wood Creek, SC, 33°18.2′N, 79°10.6′W, intertidal, coll. by GML staff, 21 July 1970. SERTC #S781, two females, north bank of Crabhaul Creek, North Inlet, Georgetown, SC, 33°21.0′N, 79°11.3′W, intertidal, coll. by GML staff, 7 July 1971. SERTC #S782, one female, east bank of Old Man Creek, 500 m north of Town Creek, SC, 32°20.5′N, 79°10.5′W, 0–4 m, coll. by GML staff, 18 August 1970. SERTC #S784, one female, Charleston Harbor, SC, 32°45.0′N, 79°51.6′W, 12–18 m, coll. by GML staff, 17 May 1974. USNM 174414, one female, off Georgia, 31°13.02′N, 81°13.05′W, Sta. 5A, 11 m, box corer, coll. by Texas Instruments, Inc. for BLM/MMS, SABP, 21 February 1977. USNM 174415, two females, off Florida, 29°27′N, 081°03′W, 20 m, coll. by Texas Instruments, Inc. for BLM/MMS, SABP, Sta. 7A, 4 September 1977. USNM 174416, one female, one male, off Florida, 29°27′N, 081°03′W, 20 m, coll. by Texas Instruments, Inc. for BLM/MMS, SABP, box corer, Sta. 7A, 4 September 1977.

**Diagnosis.** (Modified from Williams, 1993.) Carapace dorsal surface anteriorly flattened, coarsely tuberculate and covered with stiff setae; postocular spine present. Rostrum well developed, large, triangular, slightly downturned, thickly covered with stiff setae dorsally, 0–8 spines ventrally; lateral projections terminating in acute spines. Eye stalks rounded, shorter than rostrum. First pereopods of approximately same size, chelate but

with greatly reduced fixed finger; carpus with two strong spines on anteromesial margin; propodus fixed finger small, distinct. Pereopod 2 simple, merus with proximal mesoventral spine, single subdistal spine dorsally. Pereopod 3 merus with cluster of spines ventrolaterally. Pereopod 4 merus unarmed. Abdominal sternites unarmed. Pleopods somewhat broad and flattened.

**Known range.** Massachusetts to southern Texas (Williams, 1993).

**Habitat.** Firm mud or mud-sand substrates; lower intertidal to 20 m (Williams, 1993).

**Remarks.** Often called the coastal mud shrimp, *U. affinis* is a common resident of the sounds and mesohaline tidal rivers systems of the SAB (e.g. see Prezant et al., 2002; Van Dolah et al.[11]). Zoea were collected in nearshore plankton samples at Folly Beach, South Carolina (DeLancey, 1984), but adults are obligate burrow dwellers. Frey and Howard (1969) picture a cast of a burrow and describe the burrows in the Sapelo Island area as typically 1–2 cm wide, 1–2 m long extending to a depth of 50 cm. They found that the burrow walls "lack the pelletoidal exterior characteristic of *Callianassa* burrows." The size of the individuals in the populations occurring along the Atlantic Seaboard is considerably larger than those in the populations known from the Gulf of Mexico (Heard, pers. observ.).

In Georgia waters, mud shrimp are a common food item of the Southern stingray, *Dasyatis americana* (Hildebrand and Schroeder, 1928), and the Atlantic stingray, *Dasyatis sabina* (Lesueur, 1824) (Dahlberg and Heard, 1969; Howard et al., 1977; Heard, pers. observ.). The hakes, *Urophycis regius* (Walbaum, 1792) and *Urophycis floridanus* (Bean and Dresel, 1884), also feed heavily on this crustacean (Sikora et al., 1972).

*Upobebia affinis* serves as host for a variety of symbionts. Two parasitic bopyrid isopods, *Progebiophilus upogebiae* (Hay, 1917) and *Orthione furcata* (Richardson, 1904), occur in the branchial chamber of *U. affinis* (Markham, 2001). In addition, the alpheid shrimp, *Leptalpheus forceps* Williams, was described from the burrows of *U. affinis* (Williams, 1965). Numerous specimens of *U. affinis*, along with specimens of *L. forceps*, were recovered from the stomach of a large American stingray (*D. americana*) caught in Wassaw Sound, Georgia (Heard, pers. observ.). McCloskey and Caldwell (1965) reported the presence of the symbiotic fungus, *Enteromyces callianassae*, in the hindgut of specimens from the Beaufort, North Carolina area. Ruppert and Fox (1988) listed additional symbionts of *U. affinis*, including the polychaete *Parahesione luteola* (Webster), the flatworm *Stylochus ellipticus* (Girard), the copepod *Hemicyclops adhaerens* (Williams), and the decapod *Pinnixia sayana* Stimpson. An unidentified tapeworm plerocercus attributed to the tetrarhynch genus *Prochristianella* Dollfus, was found in the digestive gland of specimens examined from the vicinity of Beaufort, North Carolina (Heard, pers. observ.). For a review of what is known about U. *affinis*, see Williams (1993).

[11] Van Dolah R.F., D. R. Calder, D. M. Knott, and M. S. Maclin. 1979. Effects of dredging and unconfined disposal of dredged material on macrobenthic communities in Sewee Bay, South Carolina. South Carolina Marine Resources Center Technical Report 39. 54 p. Marine Resources Research Institute, South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, SC 29422.

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